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Contributions to the study of sirenian evolution

CONTRIBUTIONS TO THE STUDY OF SIRENIAN EVOLUTION

by

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A thesis submitted for the degree of Doctor of Philosophy in the University of Bristol.

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CONTAINS A
PULLOUT

MEMORANDUM

This dissertation, which I submit for the degree of Doctor of Philosophy, is based upon three years' research carried out in the Department of Geology, University of Bristol, under the supervision of Dr. R.J.G. Savage.

I hereby declare that the work contained in this dissertation is the result of my own independent research and that any published or unpublished work of others is fully acknowledged in the text.

July, 1973

Geoffrey J. Heal
Geoffrey J. Heal

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ABSTRACT

Three sirenian genera are described from the Cenozoic of Libya - Libysiren sickenbergi gen. et sp. nov. from the Middle Eocene of Bu el Haderait, and Rytiodus zeltenensis sp. nov. and Metaxytherium sp. indet. from the Lower Miocene of Gebel Zelten. These sirenians respectively represent the first identifiable Palaeogene member of the order recorded in Africa outside of Egypt, and the first substantial evidence of the order from the Neogene of Africa. Libysiren gen. nov. is most closely allied to Protosiren (Protosirenidae), but also shows some similarities to Eotheroides and Prototherium (Eotheroididae fam. nov.); Rytiodus and Metaxytherium both belong to the Dugongidae, but to separate subfamilies - the Rytiodinae and the Metaxytherilnae respectively.

A sirenian close to Eotheroides aegyptiacum is recorded from the Eocene of southern France, representing the first definite occurrence of this genus in Europe. This new, relatively abundant, material permits a revision of certain Eocene sirenian specimens from France and Egypt.

A new specimen of the poorly known Mio-Pliocene trichechid sirenian Ribodon limbatus is recorded from Argentina.

A review of the Sirenia utilizes the most recent information to discuss the rostrum and tusks of the Dugongidae, the genera Halitherium and Metaxytherium, the origin of Dugong, and the importance of Tethys in the origin of the Sirenia. A new classification of the Sirenia includes three new superfamilies, one new family, and one new subfamily.

A study of the gross morphology and jaw musculature of the head of a dugong, Dugong dugon, serves as the basis for a functional analysis of its feeding mechanism, which is then compared with the mechanisms suggested for the manatee, Trichechus, and Eocene sirenians.

Appendices contain keys to the families, subfamilies, and genera of sirenians, and distribution maps of living and fossil sirenians.

PART ONE

FOSSIL SIRENIA

INTRODUCTION

Research on fossil members of the Sirenia (manatees, dugongs, and their extinct relatives) has been undertaken sporadically since the beginning of the nineteenth century, notably by German-speaking palaeontologists (Lepsius, 1882; Abel, 1904, 1913; and Sickenberg, 1934), but also by French (Deperet & Roman, 1920) and American (Simpson, 1932; Reinhart, 1959) workers. Interest in the fossil representatives of the order was initially focused on the nineteenth-century finds from the Oligocene and Miocene strata of Europe, then at the turn of the century it switched to the exciting Eocene specimens from Egypt, and more recently it has crossed the Atlantic with the discovery of fossil sirenians on both the east and west coasts of the Americas. The research in these different areas has tended to be carried out independently, with the resulting description of a plethora of species that could very probably have been avoided if intercontinental comparisons had been carried out.

This part of the thesis was originally envisaged solely as an account of the sirenians recovered from the Cenozoic of Libya by field parties from the University of Bristol, but as work progressed it became obvious that there were other sirenian topics that needed attention. The sirenians from Libya are interesting and important because they include a new genus, a new species of a genus that has not previously been recorded from Africa, and another genus that is new to Africa. The description and discussion of these taxa takes up the first half of this part of the thesis.

I was fortunate to be given permission to describe some Eocene sirenians that have recently been found in southern France by members of the Universiteit van Amsterdam; although they closely resemble a previously described species from Egypt, they represent our only definite connection between the Palaeogene sirenian faunas of Europe and Africa. The description of these sirenians is restricted to features that have not been adequately covered by previous authors or that conflict with the views of these authors.

A short chapter is devoted to an incomplete mandibular ramus, recently

TABLE 1 CENOZOIC TIME SCALE

TIME IN my	EPOCH / SERIES		EUROPEAN AGE / STAGE	ZONE
	PLEISTOCENE		CALABRIAN	N22—N23
1.8	PLIOCENE		ASTIAN / PIACENZIAN	N21
			ZANCLIAN	
5.0	MIOCENE	L	MESSINIAN	
			TORTONIAN	N16
10		M	SERRAVALLIAN	N15
			LANGHIAN	N8
		E	BURDIGALIAN	N7 N6
20			AQUITANIAN	N5 N4
22.5	OLIGOCENE	L	CHATTIAN	N3 N1
30		E	RUPELIAN	P19
			LATTORFIAN	P18
37.5	EOCENE	L	BARTONIAN / PRIABONIAN	P17 P15
40		M	LUTETIAN	P14 P10
50		E	YPRESIAN	P9 P7
53.5	PALAEOCENE	L	THANETIAN	P6 P3
60		E	DANIAN	P2 P1

discovered in the collections of the British Museum (Natural History), that has been reidentified as belonging to the early trichechid Ribodon.

The last chapter is an attempt to up-date Reinhart's (1959) review of the Sirenia. It contains information that has appeared since 1959 and discusses aspects of sirenian evolution that Reinhart did not consider. It ends with a new classification of the Sirenia down to generic level.

Three appendices are added to cover measurements (enlarged in the case of the Eocene sirenians to include previously unrecorded dimensions of specimens examined by the author), keys to the families, subfamilies, and genera of sirenians, and distribution maps of the fossil and living taxa (with the palaeogeography indicated in most cases).

The Cenozoic time scale used throughout this part of the thesis is based upon Berggren (1972) and is summarized in Table 1.

Acknowledgements

This thesis would not have been possible without the encouragement, help, and supervision of Dr. R. J. G. Savage. I would like to take this opportunity to thank him for providing the initial stimulus for this work, namely the sirenian material that he was instrumental in collecting in Libya. I am also grateful to him for reading and criticising a large part of the manuscript.

My work at various museums has been made possible and enjoyable by the following persons: Drs A. J. Sutcliffe and W. R. Hamilton, Department of Palaeontology, British Museum (Natural History), London; Miss B. J. Pyrah, Yorkshire Museum, York; Drs D. E. Russell and L. Ginsburg, Institut de Paleontologie, Museum National d'Histoire Naturelle, Paris; Dr. P. Y. Sondaar, Geologisch Instituut, Rijksuniversiteit te Utrecht, Utrecht; J. Smit and H. K. H. Holst, Geologisch Instituut, Universiteit van Amsterdam, Amsterdam; Dr. M. Freudenthal, Museum van Geologie en Mineralogie, Leiden; Prof. Dr. R. Dehm and Dr. F. Obergfell, Bayerische Staatssammlung für Palöontologie u. historische Geologie, Munich; and Drs J. Fransen and S.

Rietschel, Forschungsinstitut Senckenberg, Frankfurt am Main.

I am grateful to Drs C. K. R. and G. C. L. Bertram of the University of Cambridge for information on living sirenians, and to Dr. D. P. Domning of the Department of Paleontology, University of California, Berkeley, for helpful discussion on various aspects of sirenian evolution. Invaluable help, in various forms, has also been provided by my colleagues, Drs A. W. Wight, A. F. Wilkinson, and A. N. Insole, and M. J. Bishop.

Facilities were kindly provided by Professor D. L. Dineley in the Department of Geology, University of Bristol, and I would especially like to thank R. J. Godwin for his care over the photographic work in this part of the thesis and Miss M. E. Rampton for her help with Figures II and III in Appendix C.

This study was made possible by a three-year NERC Research Studentship that was held between September, 1970, and August, 1973.

GLOSSARY

The following is a short list of anatomical definitions that are not in common usage or have special reference to the Sirenia.

Facies petrosi fonticuli mastoidei

The posterior surface of the pars mastoidea, which is produced in some sirenians to fill the fonticulus mastoideus.

Foramen lacerum

In the Sirenia the foramen lacerum anterius (the foramen lacerum medium of those who call the sphenorbital canal the foramen lacerum anterius), the foramen lacerum posterius, the foramen ovale, and the stylomastoid foramen unite to form a single, large foramen lacerum (s.l.).

Metaloph(id)

The posterior loph of a bilophodont upper (lower) cheek tooth; formed in the Sirenia by metacone, metaconule, and hypocone (entoconid and hypoconid).

Pachyostosis

The phylogenetic increase in density and thickness of individual parts of the skeleton of fossil and recent vertebrates. This phenomenon is very marked in the Sirenia, with even the marrow cavities obliterated.

Pars mastoidea

As used in this work, the posterior part of the periotic.

Pars petrosa

As used in this work, that part of the periotic containing the middle ear.

Petrotympanic

The bone formed by the fusion of the periotic and the tympanic. In all sirenians (except Prorastomus) it is not attached to the squamosal.

Processus retroversus

The process on the posterior end of the zygomatic arch that is prominent in some sirenian genera.

Protoloph(id)

The anterior loph of a bilophodont upper (lower) cheek tooth; formed in the Sirenia by paracone, protoconule, and protocone (metaconid and protoconid).

Rostrum

The anterior region of the skull, formed of the enlarged premaxillae, which is especially prominent in sirenians.

Superficies meatus

The groove on the ventral surface of the squamosal that covers the tissue of the external auditory meatus.

Tegmen tympani

In the Sirenia the tegmen tympani is a bulbous, kidney-shaped feature that forms a roof over the middle ear. It is also known as the tholus or dome.

ABBREVIATIONS

Osteological

AAF anterior alisphenoid foramina
ACAF anterior capitular facet
AF anterior articular facet
AS alisphenoid(s)
ASC alisphenoid canal

BO basioccipital
BS basisphenoid

C centrum
CAF capitular facet
CBR cerebellar region
CF cotylar facet
CP cribriform plate
CR cerebral region

DA dorsal arch
DP diapophysis

EAM external auditory meatus
ECT ectoturbinal(s)
ENT endoturbinal(s)
EO exoccipital

F frontal(s)
FAI foramen acusticum inferius
FCO fenestra cochleae
FE foramen endolymphaticum
FF facial foramen
FL foramen lacerum
FM foramen magnum
FMA fonticulus mastoideus
FPFM facies petrosi fonticuli mastoidei
FV fenestra vestibuli

GF glenoid fossa

HF hypoglossal foramen

ICF infraorbital canal foramen
IVF intervertebral foramen

J jugal

L lacrimal
LCT longus colli tubercle

M maxilla(e)
MAF mandibular foramen
MAS mandibular symphysis
ME mesethmoid
MF mental foramen (foramina)
MRF mesorostral fossa

N nasal(s)
NA neural arch
NC neural canal
NF nutrient foramen (foramina)
NPF nasopharyngeal fossa
NS neural spine
NT nasoturbinal(s)
NUC nuchal crest

O occipital
OC occipital condyle
ODP odontoid process
OF optic foramen

P parietal(s)
PAF posterior alisphenoid foramen
PAP parapophysis
PCAF posterior capitular facet
PE periotic
PF posterior articular facet
PL palatine(s)
PM premaxilla(e)
PMA pars mastoidea
PMS premaxillary symphysis
POP paroccipital process
POZ postzygapophysis
PP pterygoid process

PPT	pars petrosa
PR	promontorium
PRE	processus retroversus
PRZ	prezygapophysis
PS	presphenoid
PTP	post-tympanic process
SC	spinal cord
SCF	sinus canal foramen
SFC	suprafacial commissure
SM	superficies meatus
SO	supraoccipital
SOF	sphenorbital foramen
SOP	supraorbital process of frontal
SQ	squamosal
SS	Sylvian sulcus
TC	temporal crest(s)
TCB	tentorium cerebelli
TP	transverse process
TT	tegmen tympani
TUF	tubercular facet
V	vomer
VA	ventral arch
VF	vertebrarterial foramen
ZJ	zygomatic process of jugal
ZSQ	zygomatic process of squamosal

Dental

a	alveolus
end	entoconid
hcd	hypoconid
hcld	hypoconulid
mcd	metaconid
ml	metaloph
prcd	protoconid
prl	protoloph

Museums

BM(NH)	British Museum (Natural History), London, England
BSM	Bayerische Staatssammlung für Paläontologie u. historische Geologie, Munich, Germany
GIA	Geologisch Instituut der Universiteit van Amsterdam, Amsterdam, Holland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
RGM	Rijksmuseum van Geologie en Mineralogie, Leiden, Holland
SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany
UB	Department of Geology, University of Bristol, Bristol, England

On many of the figures in this thesis stippling and hatching represent matrix and broken (or cut) surfaces respectively.

CHAPTER 1: FOSSIL SIRENIA FROM LIBYA

HISTORICAL BACKGROUND AND GEOLOGY

Cenozoic mammal material was first found in Libya by Desio in 1931, and it was subsequently described by D'Erasmo (1934). This initial find (an indeterminate ungulate) at Gasr es Sahabi led to further investigation of the surrounding area and a good mammalian fauna is now known. The age of the Sahabi deposit is believed to lie between 5 and 6 my B.P. on the basis of the presence of Stegotetrabelodon syrticus (Maglio, 1970).

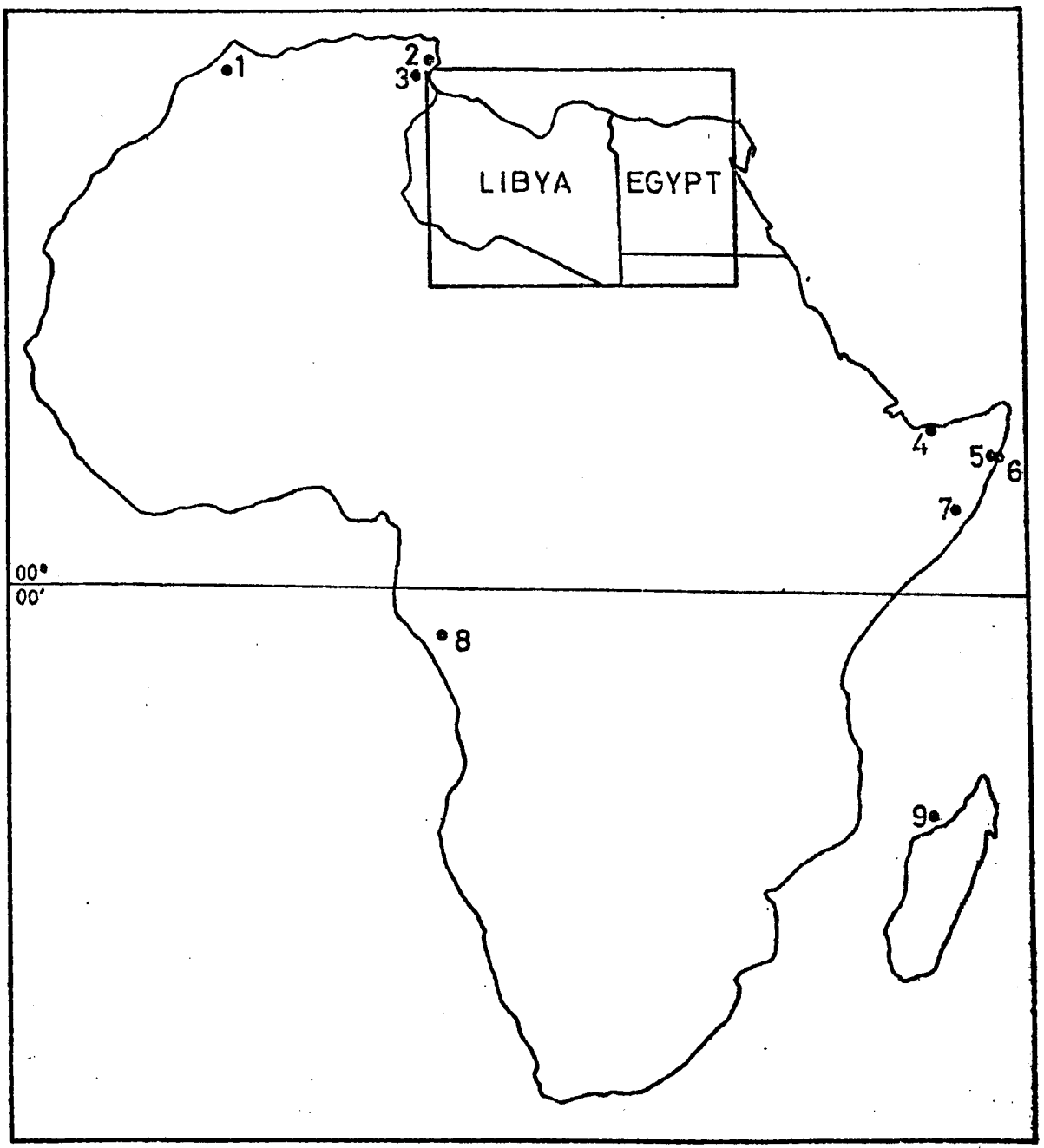
The occurrence of mammals at the Miocene locality of Gebel Zelten was first reported by Arambourg & Magnier (1961), and Arambourg described the varied elements of the fauna (1961a, 1961b, 1963b). In a short geological description of the mammal-bearing strata at Gebel Zelten, Magnier (1962) made the first reference to the presence of fossil sirenians in Libya:

> '-les niveaux 7 et 8 se caracterisent paléontologiquement par de nombreux restes de Siréniens impliquant un milieu de vie en eau peu salée.'

The gebel was later visited by an expedition from the University of Bristol, led by Dr. R.J.G. Savage, which had the aim of collecting more mammalian material. This expedition (in 1964) was so successful that it stimulated several more during the late 1960's, and thus a very large collection of Libyan fossil mammals was established at Bristol. Although special attention was paid to the collection of terrestrial mammals, Dr. Savage and his co-workers also brought back sirenian remains in 1966 and 1967. Several of the terrestrial mammal groups from Gebel Zelten have already provided theses' topics for postgraduate workers at Bristol; Harris (1969) described the proboscidean material, Hamilton (1972) described the ruminants, and Wilkinson (1972) dealt with the suids.

An Oligocene horizon near Zella was visited by the French in 1959 and 1960 (Arambourg & Magnier, 1961; Arnould-Saget & Magnier, 1961), and has yielded two early proboscideans, Palaeomastodon and Phiomia. This horizon lies

FIG. 1
AFRICA: SIRENIAN LOCALITIES



1. Dar bel Hamri, Morocco (Pliocene)
2. Djebel ech Cherichira, Tunisia (Oligocene)
3. Bled Douarah, Tunisia (Miocene)
4. Daban, Somali Republic (Eocene)
5. Callis, Somali Republic (Eocene)
6. Bedei, Somali Republic (Oligocene)
7. Mogedishu, Somali Republic (Eocene).
8. Malembe, Congo (Miocene)
9. Ile Makamby, Malagasy Republic (Miocene)

0 1000 2000
KM

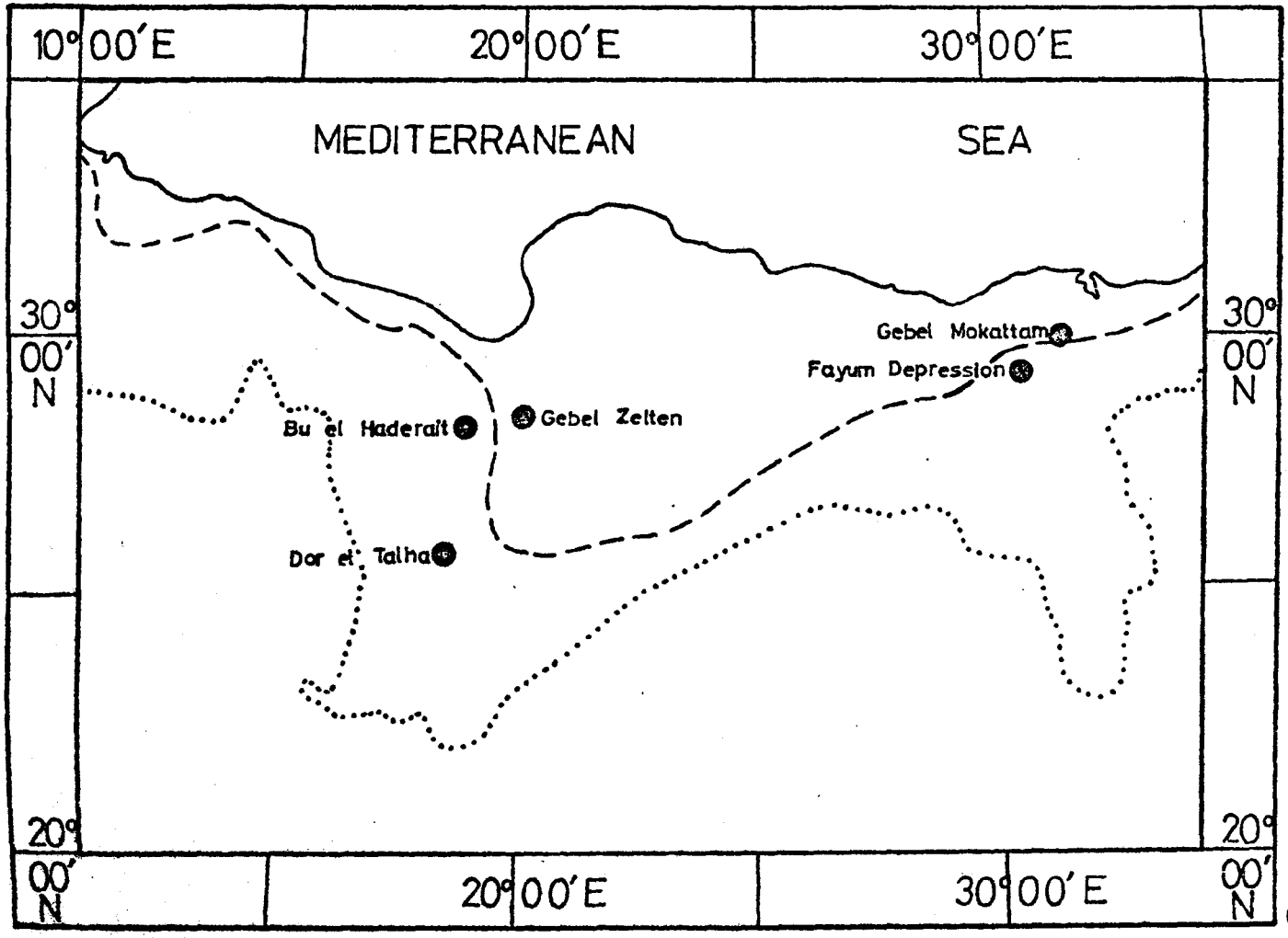
above the Graret el Gifa Member (Lutetian-Priabonian) of the Wadi Tamet Formation.

Eocene mammals from Dor el Talha ("Gebel Coquin" of some earlier workers) were first recorded by Arambourg & Magnier (1961) and Arambourg (1963a). This locality was visited by University of Bristol field-parties in 1968 and 1969 (Savage, 1969), and Wight (1971) has described its geology and proboscidean fauna. The latter author concluded that the Dor el Talha mammals include both Eocene and Oligocene species. Sirenian rib fragments were found at Dor el Talha in 1968. The new Eocene locality of Bu el Haderait has yielded no terrestrial mammals, but sirenians are relatively abundant there (Savage & White, 1965).

More detailed information on these Libyan fossil mammal localities can be obtained from Savage (1971) and Savage & Hamilton (1973), and from the previous theses in this series (Harris, 1969; Hamilton, 1970; Wight, 1971; Wilkinson, 1972).

The Sirte Basin of northern and central Libya was formed by intensive block faulting during the Mesozoic (Late Cretaceous) and Cenozoic (Klitzsch, 1968). It lies between the Tethyan foredeep and the Saharan platform, and is bordered on the west, south, and east by the Haroudj, Tibesti-Sirte, and Calanscio-Auenat uplifts respectively. During the Cenozoic, marine transgressions and regressions filled the basin with a thick sequence of clastics, carbonates, and minor evaporites, which have a total thickness of at least 5,000m in the centre of the basin. The Cenozoic strata range in age from Palaeocene (Danian) to Late Miocene (Messinian). The Sirte Basin reached its largest extent during the Palaeocene and Eocene, when its shoreline was located approximately 850km from the present Libyan coast; however, by the beginning of the Neogene the sea had retreated northwards to within 450km of the present coast (Desio, 1971) (see Fig. 2). The three sirenian localities dealt with in this chapter are situated close to these ancient shorelines, and two of them have also yielded land mammals.

FIG. 2



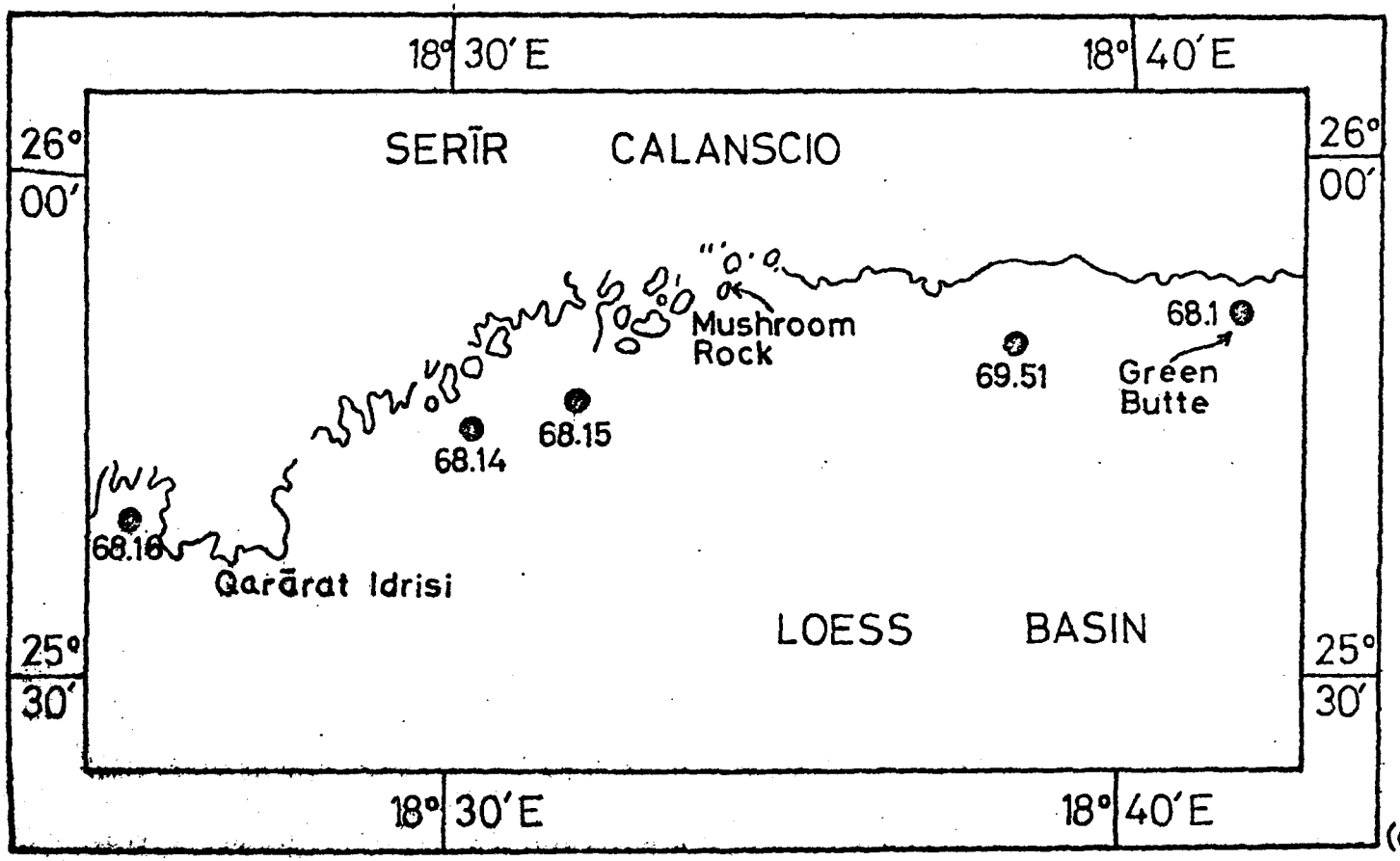
LIBYA AND EGYPT: SIRENIAN LOCALITIES.

(adapted from Desio, 1971, fig.2)

Bu el Haderait (28° 15' N., 18° 30' E.) is probably the earliest Cenozoic mammal locality on the African continent, and here sirenian skeletons are associated with foraminiferans, bryozoans, molluscs, arthropods, and echinoderms (Savage & White, 1965). These organisms are preserved in a whitish calcilutite that is interbedded with mollusc-rich limestones and capped by a sandstone. The whole succession is c.30m thick, and the strata are horizontal. The most characteristic invertebrate fossil of the calcilutite is the large foraminiferan Nummulites laevigatus (Brug.), which is generally accepted as one of the guide fossils of at least the lower part of the Lutetian of the Paris Basin (Berggren, 1967). This distinctive species has also been recorded from a 'white-yellowish chalk' in Cyrenaica that is overlain by a sequence of massive limestones containing Nummulites discorbinus Schloth., N. gizehensis Ehr., etc. (Desio, 1968). The latter species is found throughout the upper part of the Lutetian of North Africa - Mokattam Formation of Egypt (Said & Martin, 1964, fig. 4); Wadi Rayan Formation of the Fayum Depression, Egypt (Beadnell, 1905); Apollonia, Derna, and Slonta Formations of Libya (Kleinsmiede & van den Berg, 1968; Pietersz, 1968). N. laevigatus therefore appears to occupy a similar position in the stratigraphic sequences of both the Paris Basin and the Sirte Basin, and the beds that yield sirenians at Bu el Haderait can be placed in the lower part of the Middle Eocene (Lutetian). These strata are therefore a southern equivalent of the lower part of the Wadi Tamet Formation of the northern Sirte Basin.

The stratigraphy of Dor el Talha (25° 45' N., 18°-19° E.) has been investigated by Wight (1971), who has recognized four units therein. Principally by correlating the land mammal faunas of the Dor el Talha sequence with those from the Palaeogene deposits of the Fayum Depression, Egypt, he has placed the Qarārat and Raqaba Units of the former in the Upper Eocene, and the Idam and Serir Units in the Oligocene. The succession consists of gypsiferous silts, rhythmic alternations of sands and silts, oyster banks, and a sandstone cap at the top. Sirenian ribs occur in the

FIG. 3



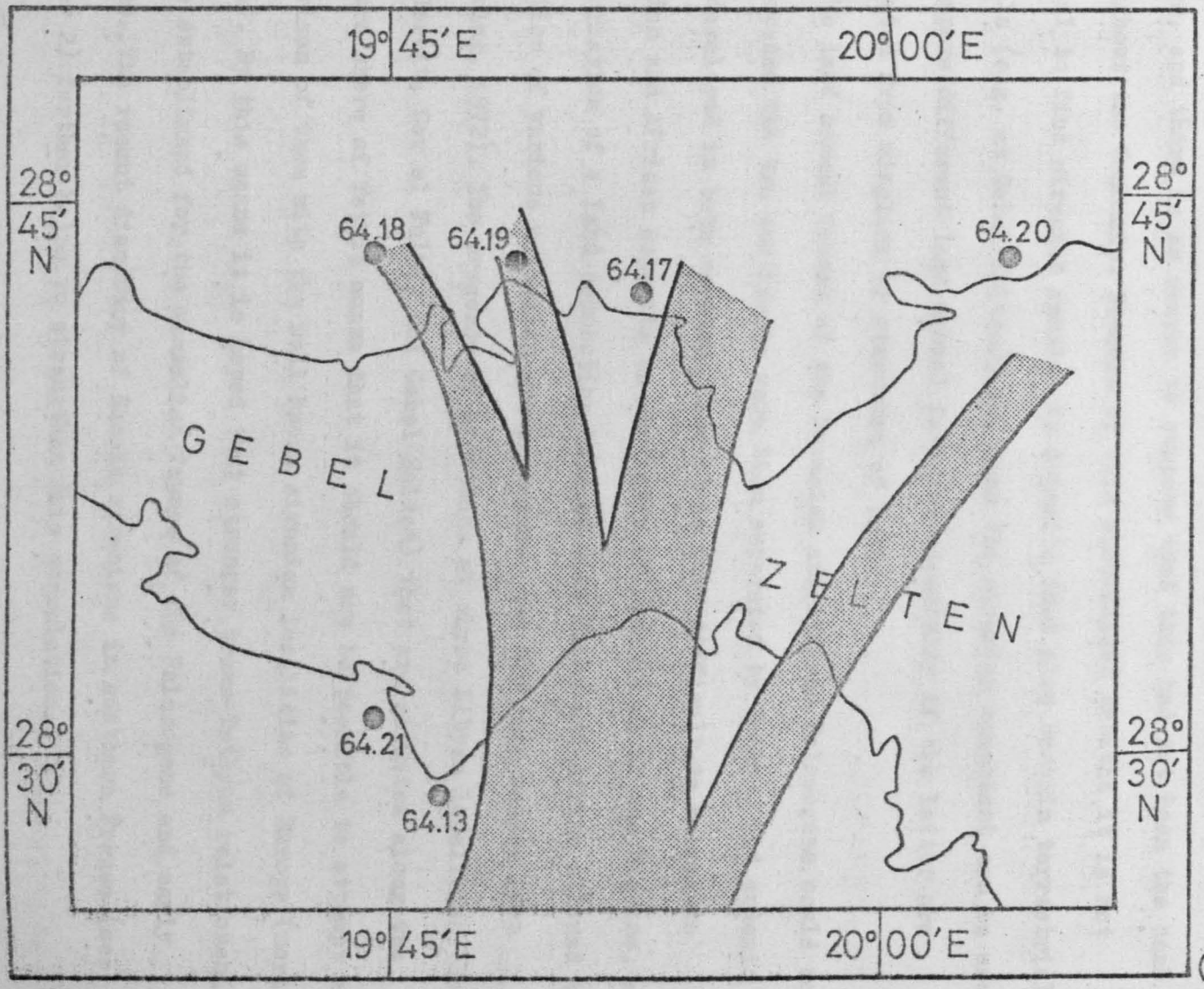
DOR EL TALHA: SIRENIAN SITES.

(adapted from Wight, 1971, fig.2.2)

gypsiferous mudstones of the Raqaba Unit, and this places them at an equivalent level to the sirenians from the Qasr el-Sagha Formation of the Fayum Depression (Wight, ibid.). (see Fig. 3).

Gebel Zelten (28°-29° N., 19° 30'-20° 30' E.) has received the most attention of the three localities. Its mammal fauna has been studied by both Arambourg and workers at the University of Bristol, and its sedimentology and palaeoecology have been investigated by Selley (1966, 1967, 1969, 1971) and Doust (1968) respectively. The Miocene Marada Formation at Gebel Zelten consists of alternating limestones, sandstones, and shales (Selley, 1966). In general, marine limestones become more abundant northwards and continental sandstones and unconsolidated sands increase in importance southwards. This sequence is interrupted by sandstone channels that were interpreted by Selley (1966) as river courses, and the distribution of sirenian remains at Gebel Zelten approximately coincides with these channels and the edges of the lagoonal facies (Savage, in Selley, 1969). Selley (1966) compared the environment at Zelten during the Miocene to that of the present-day coast of Texas - a region from which sirenians have been recorded within historic times. The age of the Zelten deposits has been the subject of some controversy, but most authors have favoured a Burdigalian, or equivalent, age. Savage & Hamilton (1973) concluded that the Gebel Zelten mammal fauna was early Burdigalian in age, although Harris (1969) thought that a late Burdigalian age was more applicable. Hamilton (1970) has compared the Gebel Zelten mammal taxa with those from other African Miocene localities, and he concluded that the Zelten fauna indicates an early Burdigalian age. Wilkinson (1972) identified a suid species, Xenochoerus africanus (Strom.), that is common to both Gebel Zelten and several East African localities (Rusinga Island, Mfwanganu Island, Songhor, Karungu, and Bukwa). Radiometric ages have been obtained for these latter localities (Bishop et al., 1969; Van Couvering & Miller, 1969) and they all fall within the range of 17.5 to 23.0 my B.P., i.e. latest Oligocene-Early Miocene (Burdigalian). All of this evidence indicates that we are dealing with an horizon that is close to the Aquitanian-Burdigalian

FIG. 4



GEBEL ZELTEN: SIRENIAN SITES.

major estuarine channel of Miocene river

0 10 20 KM

(adapted from Selley, 1966, fig.14)

boundary. (see Fig. 4).

The importance of the sirenian elements in the Libyan Cenozoic faunas cannot be overemphasized. Besides the brief note of Magnier (1962), other references to sirenian remains are contained in Savage's reports (1965, 1969, 1971); however, these are merely notes on the presence of remains at the different localities. The value of fossil sirenians is related to their occurrence in marine, estuarine, and fluviatile deposits, and therefore to their use as correlatives between discontinuous land areas. Modern sirenians, unlike most cetaceans, are predominantly inhabitants of coastal and fluvial waters, and there is no reason to suppose that this has not been the case throughout the Cenozoic. Because of this specialized habitat it is not unusual to find sirenian remains in deposits that also contain terrestrial mammals (e.g. at Gebel Zelten), and then the sirenian component can be used to compare different land mammal faunas - especially if the latter are prevented from mingling by stretches of water.

The land mammal faunas of the Eurasian and African Palaeogene could not mix because the two continents were then separated by Tethys, and endemic taxa developed in both regions. Thus it is very difficult to correlate Eurasian and African deposits on the basis of mammals until the Miocene, when the formation of a land connection between Asia Minor and Africa allowed the migration of various mammalian groups between the two land masses (Van Couvering, 1972). The presence of sirenians at three Libyan localities (Bu el Haderait, Dor el Talha, and Gebel Zelten) that are situated along the southern shore of Tethys means that it should now be possible to attempt a comparison of them with the well known sirenian localities of Europe (northern Tethys). By this means it is hoped that stronger trans-Tethyan relationships can be established for the mammalian faunas of the Palaeogene and early Neogene. The recent discovery of Eocene sirenians in southern France (see Chapter 2) further helps to strengthen this correlation.

SITE TERMINOLOGY

The Eocene, Oligocene, and Miocene sites in Libya that have been visited by parties from the University of Bristol have all been given numbers. These numbers consist of the last two figures of the year of discovery of the site followed by the site's individual number, e.g. 64.08, 69.54. In this system 64.24 includes specimens that have lost their original numbers or were presented by oil company personnel.

SYSTEMATIC DESCRIPTIONS

Order SIRENIA Illiger 1811

Diagnosis: Aquatic mammals. Premaxillae form a rostrum that is deflected in later forms; external nares dorsal; nasals prominent in primitive forms, but decrease in size as the mesorostral fossa enlarges; periotic isolated from rest of braincase in all genera except Prorastomus; tympanic semicircular. Number of incisors becomes progressively reduced; cheek teeth primitively bilophodont, but show great morphological variation in the different sub-families. Hind limbs become reduced and functionless; fore limbs become paddle-like. Tail with horizontal fluke.

Remarks: In this work the Sirenia is subdivided into three superfamilies, the Prorastomoidea, the Trichechoidea, and the Dugongoidea. This new classification is defended later in the thesis.

Superfamily PRORASTOMOIDEA superfam. nov.

Diagnosis: Rostrum slightly deflected; large nasals form anterior part of skull roof. Complete eutherian dental formula; incisor tusks begin to enlarge in some genera. Hind limbs function as paddles.

Remarks: This superfamily contains three Eocene families, the Prorastomidae, the Protosirenidae, and the Eotheroididae.

Family PROTOSIRENIDAE Sickenberg 1934

Diagnosis: Lacrimal foramen and duct absent (at least in Libysiren); alisphenoid canal present; elongated superficies meatus; processus fonticulus present; periotic isolated from rest of braincase. Incisor tusks beginning to enlarge.

Remarks: Contains the genera Protosiren and Libysiren.

Genus LIBYSIREN gen. nov.

Diagnosis: Very large protosirenid. Large nasals; prominent lacrimal bone, but no trace of lacrimal foramen or duct; sagittal length of parietals much greater than that of frontals; no temporal crests; squamosal with prominent post-tympanic process. Tentative dental formula $\frac{3}{3}, \frac{1}{1}, \frac{4}{4/5}, \frac{3}{3}$.

Etymology of generic name: Liby- from Libya: -siren from Siren (Latin) - a sea-nymph who lured mariners to destruction.

Type species: L. sickenbergi gen. et sp. nov.

Distribution: Middle Eocene (Lutetian) of Bu el Haderait, Libya.

Libysiren sickenbergi sp. nov.

Diagnosis: As for genus.

Etymology of specific name: In honour of Dr. O. Sickenberg, who has contributed greatly to our knowledge of Tertiary sirenians.

Holotype: BM(NH) M19100a-g. Skull, mandible, and associated vertebrae and ribs.

Paratypes:

UB 20607	skull roof
UB 20608	rostrum (premaxillae, maxillae, vomer)
UB 20609	mandible
UB 20610	right mandibular ramus
UB 20611	left mandibular ramus
UB 20612	left mandibular ramus
UB 20613	right mandibular ramus
UB 20614	tooth fragments
UB 20615	right M_2 and M_3

Age and locality: Middle Eocene (Lutetian) of Bu el Haderait (28° 15' N.,

18° 30' E.), Libya.

Remarks: All material assigned to this species came from the same horizon and was associated with an invertebrate fauna that included:

Protozoa

Nummulites laevigatus(Bruguière)

Nonion sp.

Elphidium sp.

Bryozoa

Several epizoic species.

Mollusca

Pelecypoda

Ostreacea

Gastropoda

Volutacea

Cephalopoda

Nautilida

Arthropoda

Crustacea

Palaeocarpilius sp.

a xanthid

Echinoderma

Echinoidea

Echinolampas crameri de Loriol

E. globulus Laube

E. fraasi de Loriol

Schizaster cf. S. gaudryi de Loriol

?Eupatagus lefeburei (de Loriol)

Echinocyamus sp.

The Protozoa were identified by W. Berggren (Woods Hole) and J. Murray (Bristol), the Arthropoda by J. Collins (London), and the Echinoderma by E. Rose (London).

This fauna suggests a shallow-water marine environment for the sirenian horizon.

Anatomical description:

Skull (Plates 1 and 6):

This description of the skull is based on material belonging to three adult individuals. The most complete specimen (M19100a) is very well preserved and is not crushed; however, all of the teeth, the right jugal, part of the right supraorbital process, and the thin walls of the orbits are missing. The second specimen (20607) consists of most of the skull roof of a larger individual with the nasals, frontals, parietals, supraoccipital, exoccipitals, and left squamosal preserved. It is possible to study the nasal chamber and the internal structure of the braincase in this specimen because the basicranium is completely missing. The third specimen (20608) consists of the premaxillae, parts of the maxillae, and the vomer; the premaxillae are better preserved than those of M19100a.

Premaxillae (Plates 1, 2, 3, and 6):

The premaxillae of M19100a are complete dorsally, but the whole of their ventral surface is missing due to extensive erosion; however, the positions of the alveoli can be seen on 20608.

The premaxillae form a prominent rostrum that tapers to a point anteriorly. The premaxillary symphysis constitutes one-third of the total length of the premaxillae, and the premaxillary rami extend posterodorsad from the symphysis so that they rest on anterior extensions of the maxillae. Each ramus narrows posteriorly and its posterior extremity abuts against the lacrimal and the nasal. The premaxillae thus enclose a large mesorostral fossa that is widest posteriorly.

Maxillae (Plate 4):

The maxillae extend from just behind the premaxillary symphysis to at least the posterior surface of M^3. The anterior part of each maxilla is produced into a support for the corresponding premaxilla, and the dorsal surface of this extension is grooved to receive the latter bone. A lateral extension of the maxilla forms the medial part of the floor of the orbit and is penetrated anteroposteriorly by the infraorbital canal (c.15mm in diameter).

PLATE 1

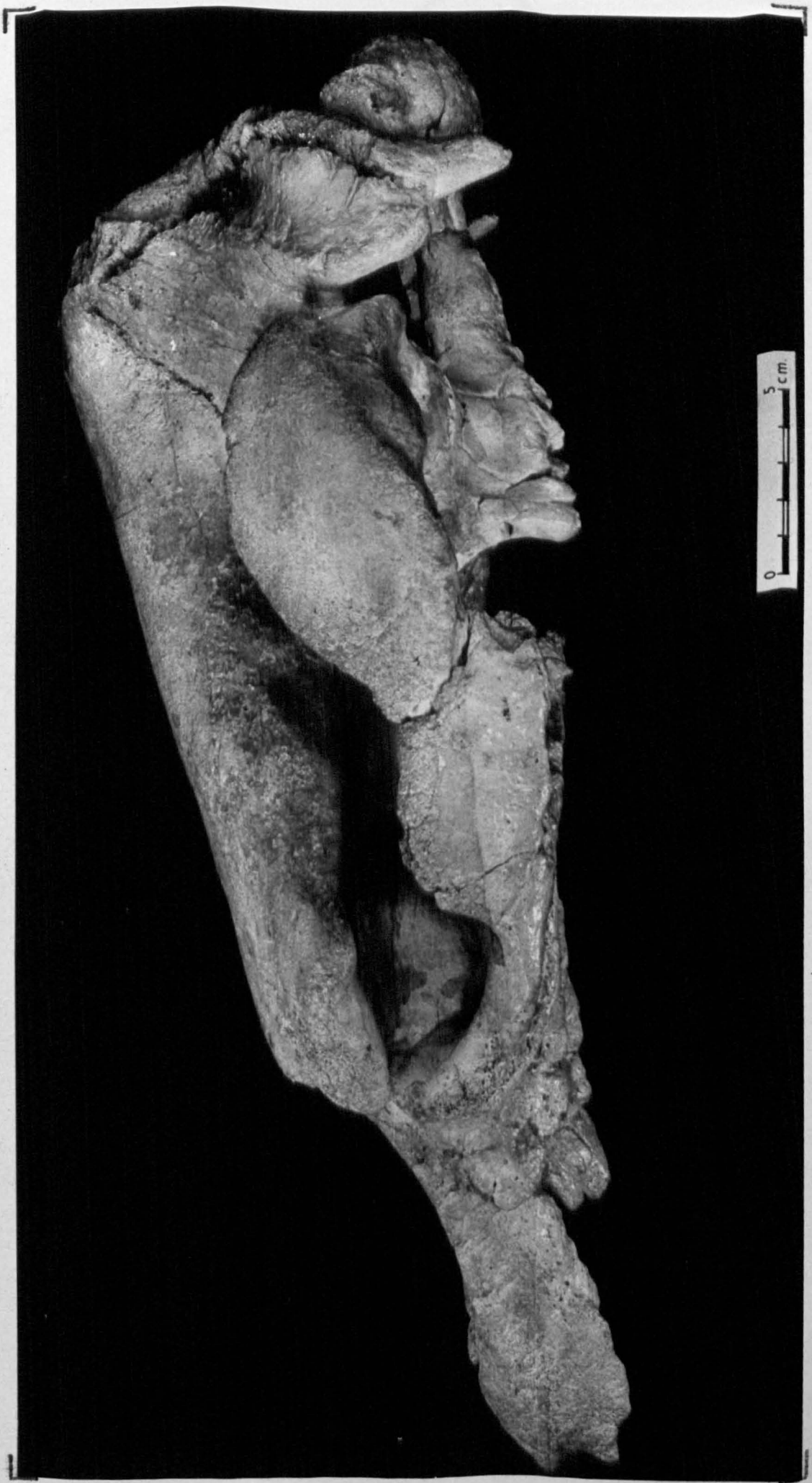
Libvairan sickenbergi gen. et sp. nov.

M19100a : left lateral view of skull

FIGURE 5

Drawing of Plate 1

PLATE 1



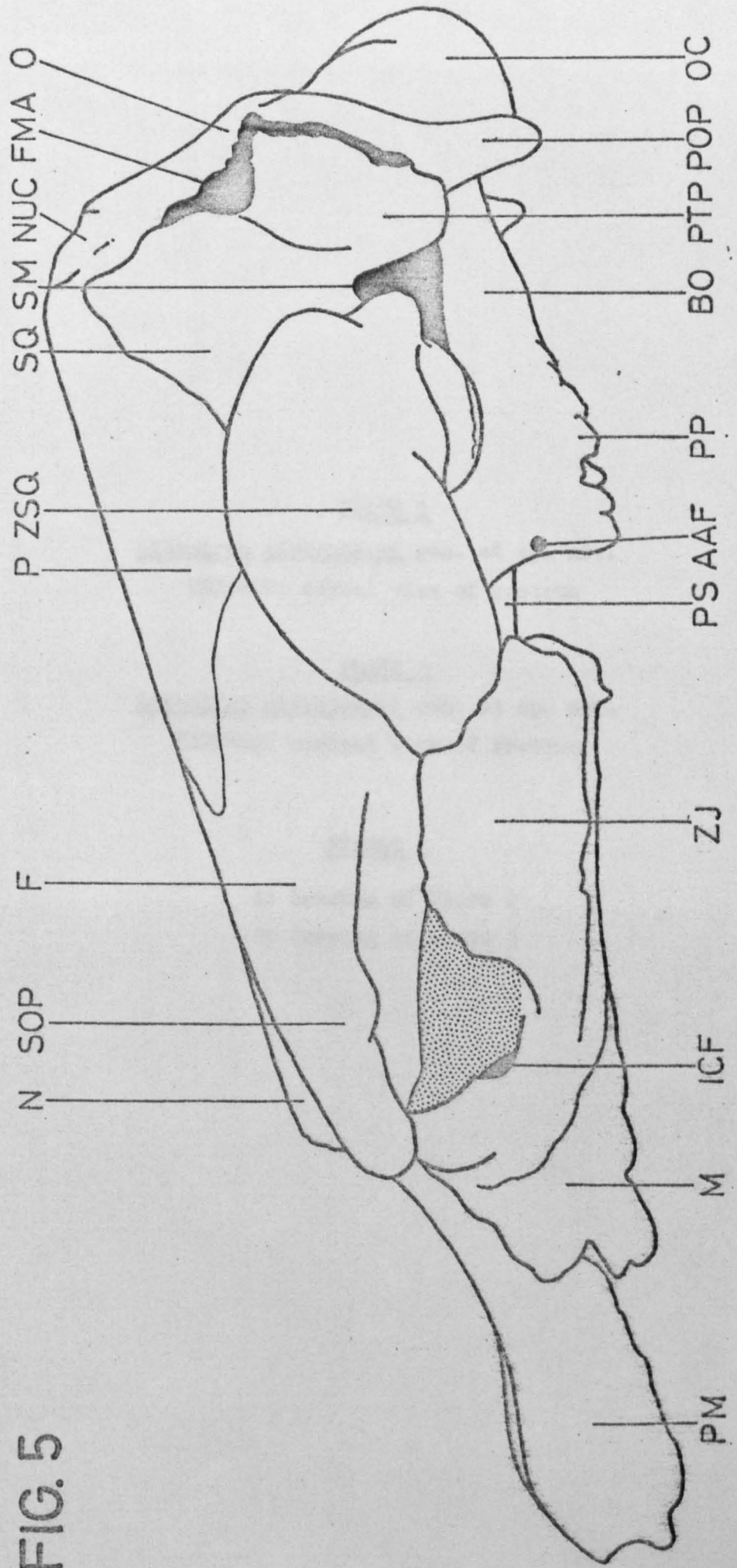


FIG. 5

PLATE 2

Libysiren sickenbergi gen. et sp. nov.

UB20608: dorsal view of rostrum

PLATE 3

Libysiren sickenbergi gen. et sp. nov.

UB20608: ventral view of rostrum

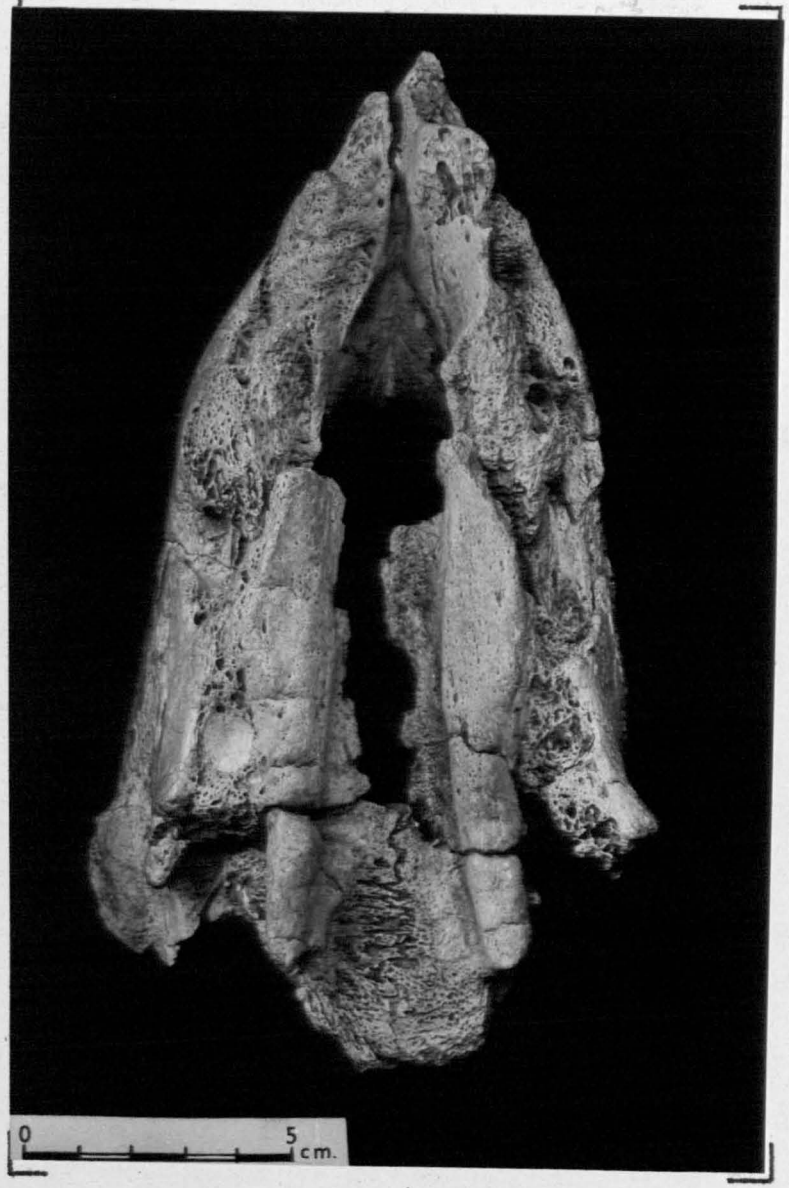
FIGURE 6

A: Drawing of Plate 2

B: Drawing of Plate 3

PLATE 2

PLATE 3



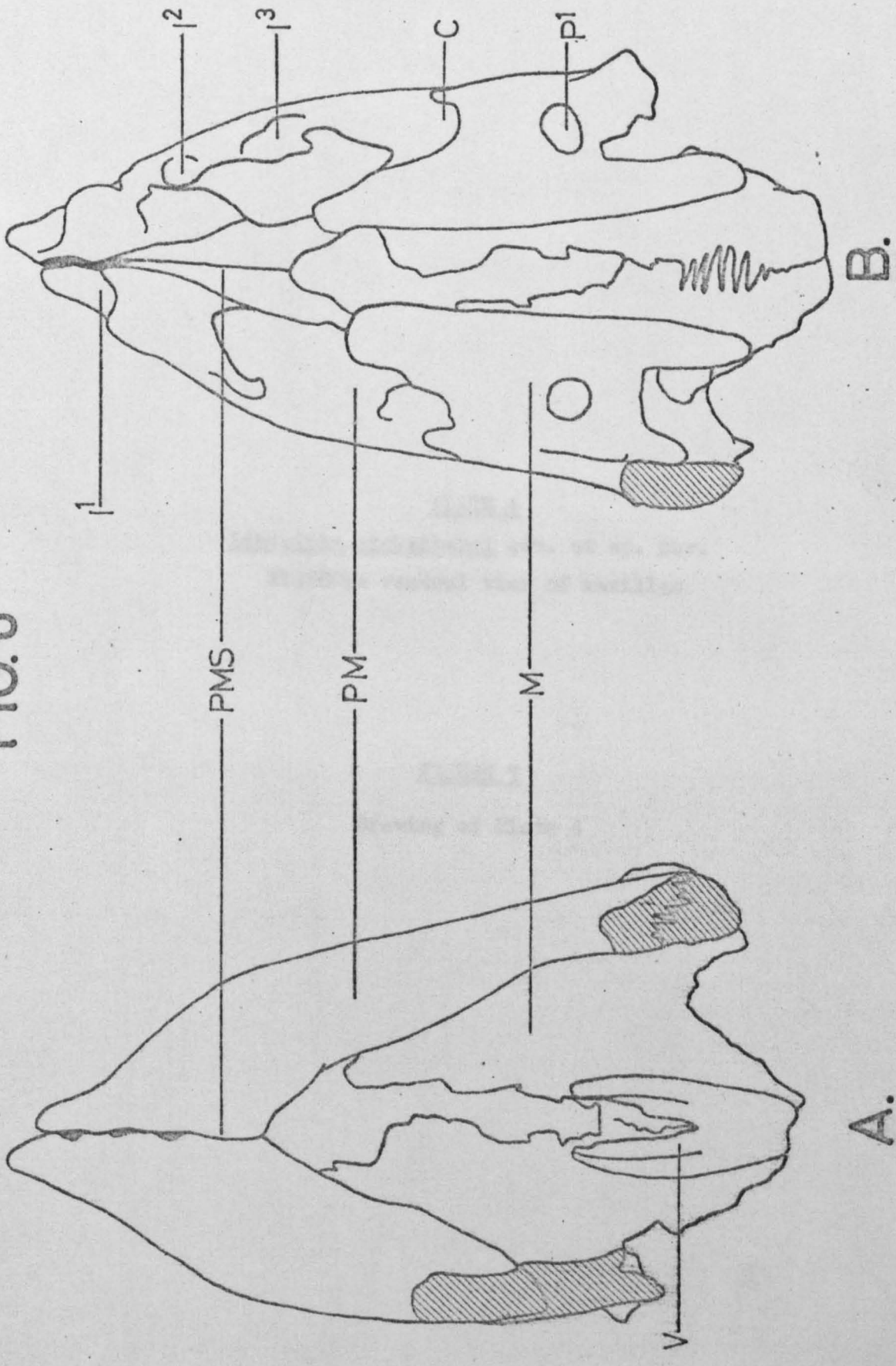


FIG. 6

PLATE 4

Libvairan sickenbergi gen. et sp. nov.

M19100a: ventral view of maxillae

FIGURE 7

Drawing of Plate 4

PLATE 4

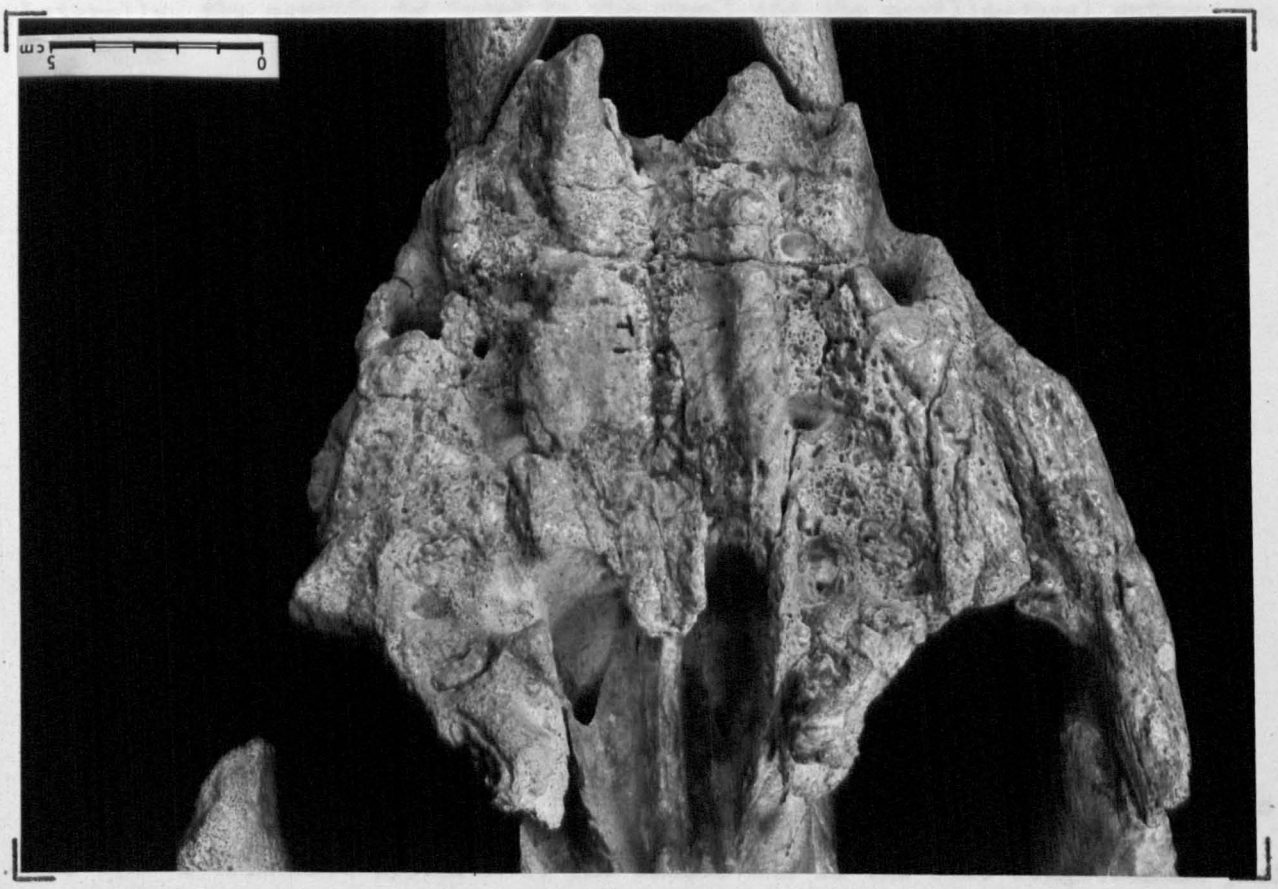
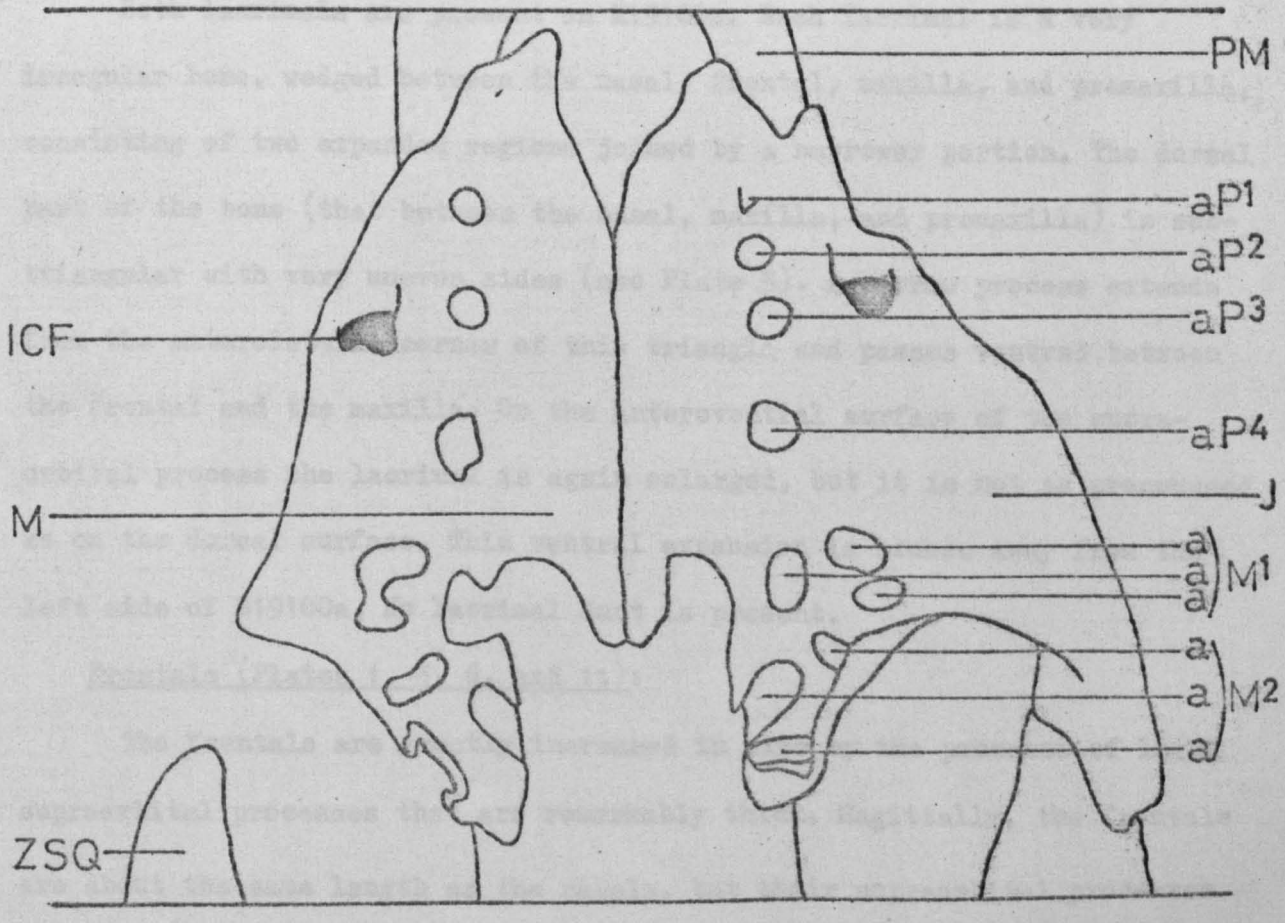


FIG. 7



Laterally, the maxilla is fused to the jugal and the maxillo-jugal suture can be traced on the right side of M19100a because the jugal is absent. Medial to each of the tooth rows there is a flat-topped ridge that reaches as far forwards as the anterior edge of the canine alveolus (20608) and as far backwards as the broken edge of the maxilla (M19100a). These two ridges may be the result of the weathering of the bone around the alveoli.

Nasals (Plates 5, 6, and 11):

The nasals are complete in M19100a, but in 20607 their anterior portions are absent. Dorsally, the nasals have an irregular outline that is exaggerated by a thin median continuation of the frontals overlying the nasals posteriorly (see Plate 5). In 20607 this frontal process is missing, but a corresponding depression in the nasals indicates that it was originally present. The anterior margin of each nasal is irregular and gives the bone a crenulate appearance. The nasals lie in the same longitudinal plane as the frontals and parietals, but they are curved downwards laterally so that they contact the lacrimals and the supraorbital processes of the frontals.

Lacrimal (Plates 5 and 6):

Both lacrimals are present on M19100a. Each lacrimal is a very irregular bone, wedged between the nasal, frontal, maxilla, and premaxilla, consisting of two expanded regions joined by a narrower portion. The dorsal part of the bone (that between the nasal, maxilla, and premaxilla) is sub-triangular with very uneven sides (see Plate 5). A narrow process extends from the anterolateral corner of this triangle and passes ventrad between the frontal and the maxilla. On the anteroventral surface of the supra-orbital process the lacrimal is again enlarged, but it is not as pronounced as on the dorsal surface. This ventral expansion is broken away from the left side of M19100a. No lacrimal duct is present.

Frontals (Plates 1, 5, 6, and 11):

The frontals are greatly increased in size by the presence of large supraorbital processes that are remarkably thick. Sagittally, the frontals are about the same length as the nasals, but their supraorbital processes

PLATE 5

Libysairen sickenbergi gen. et sp. nov.
M19100a: nasal region

FIGURE 8

Drawing of Plate 5

PLATE 5

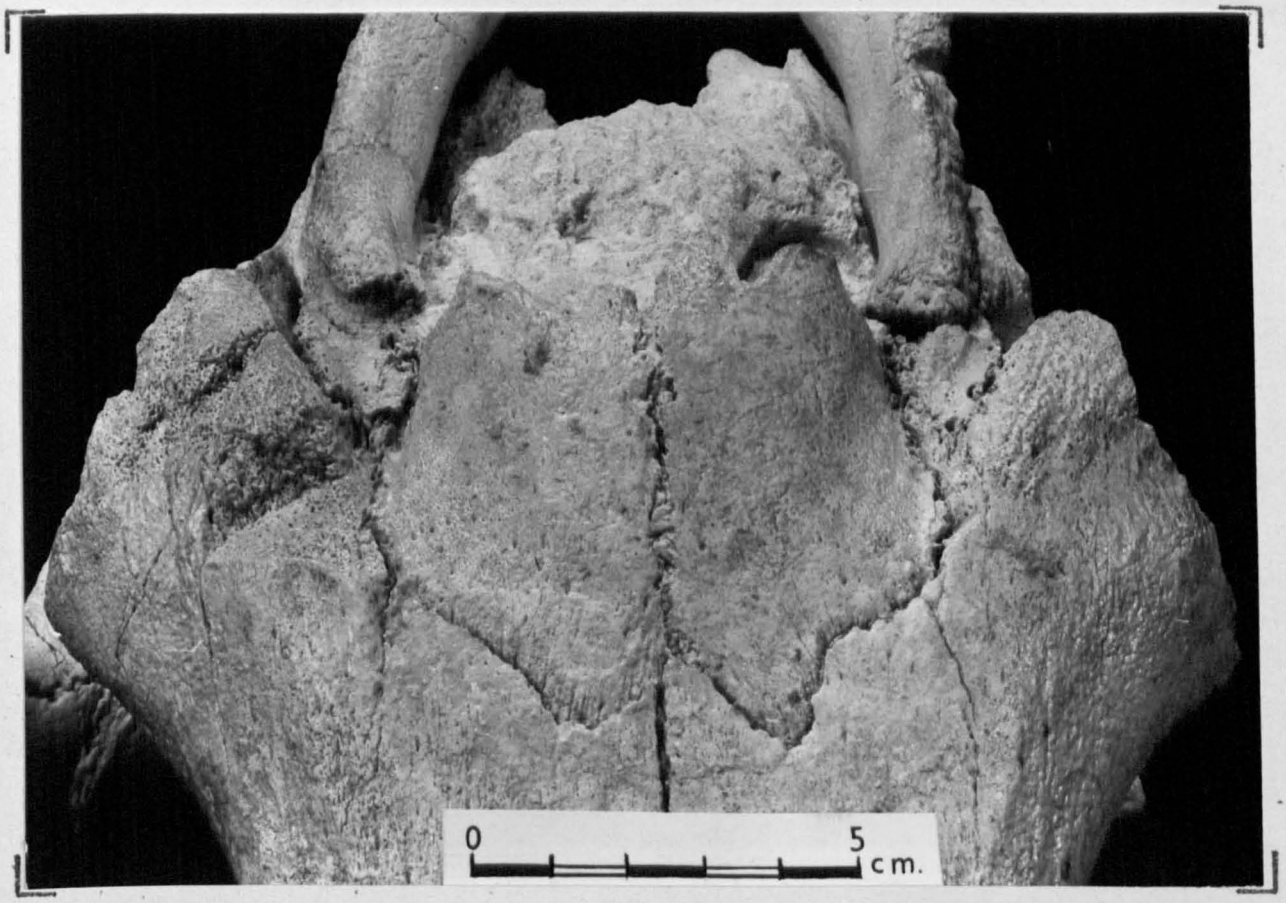


FIG. 8

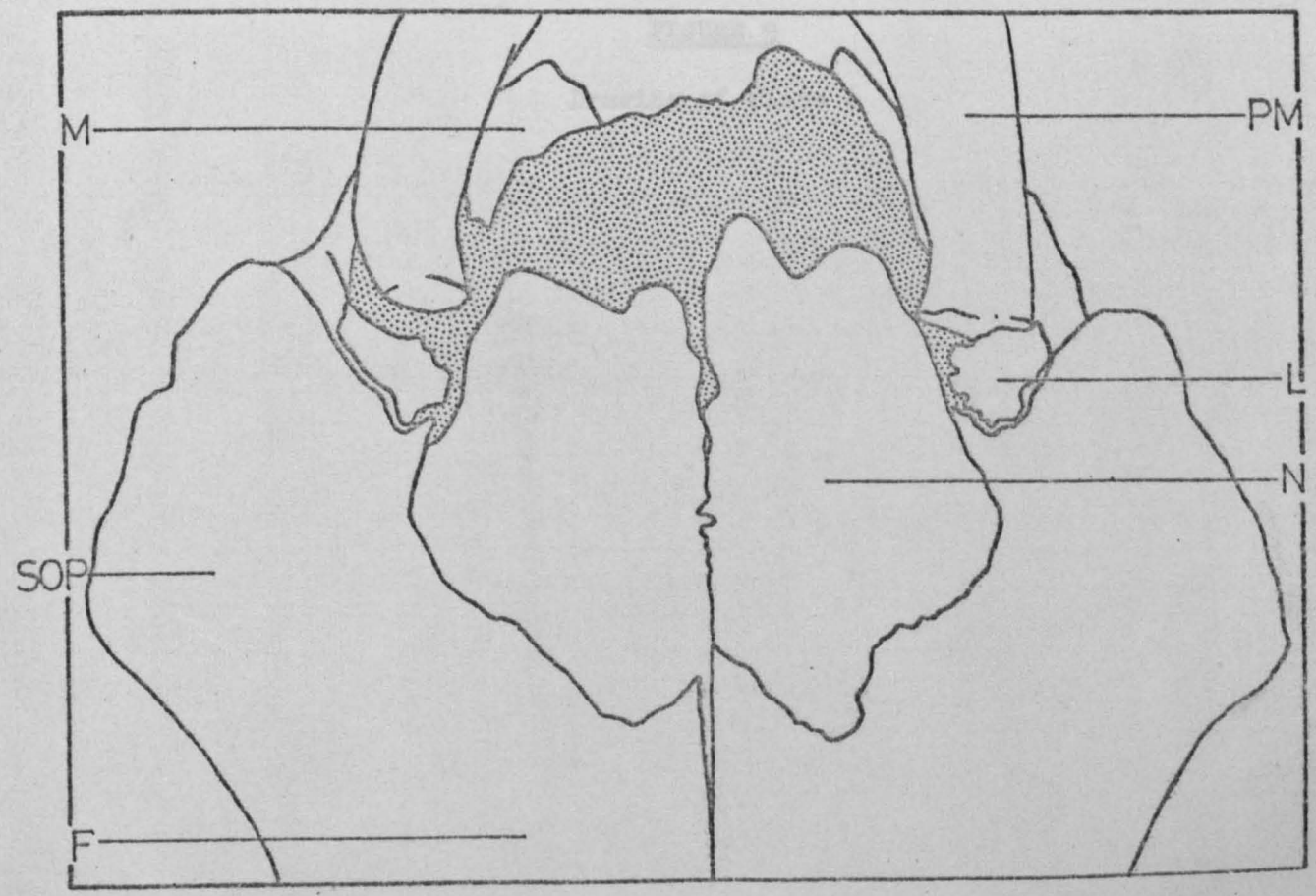


PLATE 6

Libvairan sickenbergi gen. et sp. nov.

M19100a: dorsal view of skull

FIGURE 9

Drawing of Plate 6

PLATE 6

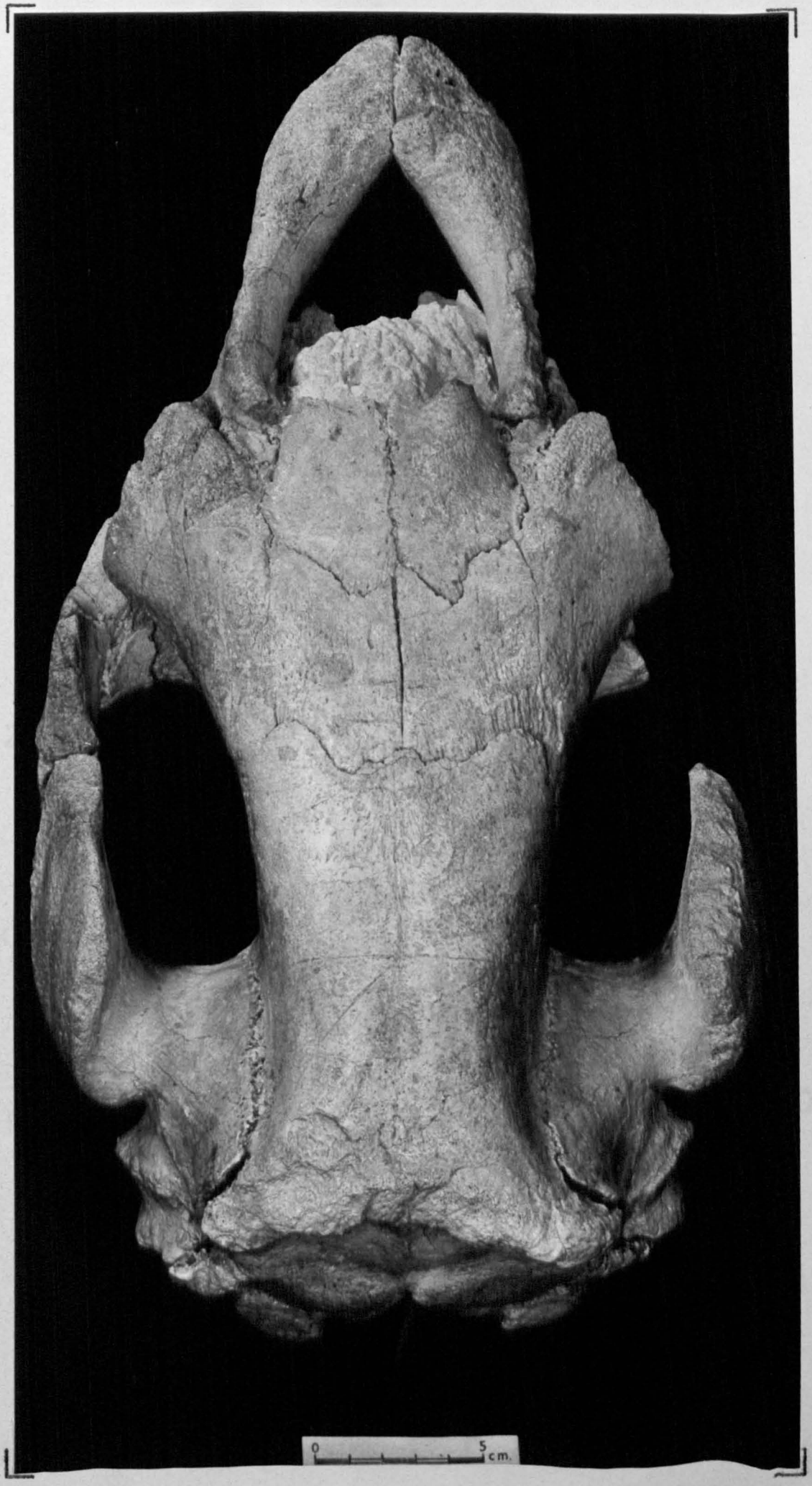
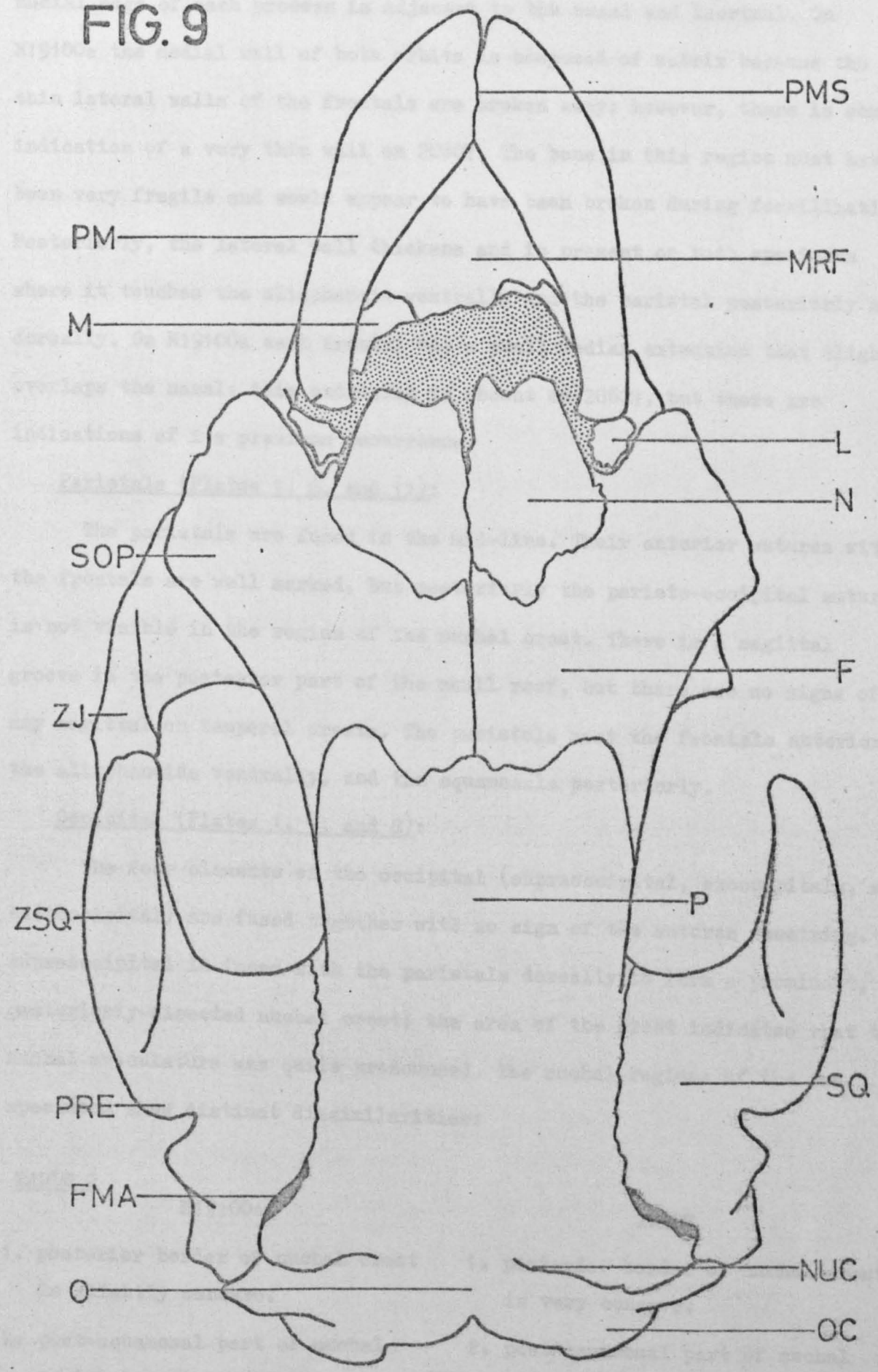


FIG. 9



extend anterolaterad to reach in front of the nasals and lacrimals. The medial edge of each process is adjacent to the nasal and lacrimal. On M19100a the medial wall of both orbits is composed of matrix because the thin lateral walls of the frontals are broken away; however, there is some indication of a very thin wall on 20607. The bone in this region must have been very fragile and would appear to have been broken during fossilization. Posteriorly, the lateral wall thickens and is present on both specimens where it touches the alisphenoid ventrally and the parietal posteriorly and dorsally. On M19100a each frontal has a small median extension that slightly overlaps the nasal; this extension is absent on 20607, but there are indications of its previous occurrence.

Parietals (Plates 1, 6, and 11):

The parietals are fused in the mid-line. Their anterior sutures with the frontals are well marked, but posteriorly the parieto-occipital suture is not visible in the region of the nuchal crest. There is a sagittal groove in the posterior part of the skull roof, but there are no signs of any sagittal or temporal crests. The parietals meet the frontals anteriorly, the alisphenoids ventrally, and the squamosals posteriorly.

Occipital (Plates 1, 7, and 8):

The four elements of the occipital (supraoccipital, exoccipitals, and basioccipital) are fused together with no sign of the sutures remaining. The supraoccipital is fused with the parietals dorsally to form a prominent, posteriorly-directed nuchal crest; the area of the crest indicates that the nuchal musculature was quite pronounced. The nuchal regions of the two specimens show distinct dissimilarities:

TABLE 2

M19100a	20607
1. posterior border of nuchal crest is slightly concave.	1. posterior border of nuchal crest is very concave.
2. post-squamosal part of nuchal region is not expanded.	2. post-squamosal part of nuchal region is expanded.

TABLE 2 (cont.)

M19100a	20607
3. a narrow median ridge extends halfway down supraoccipital from crest.	3. no median ridge, but a slight tuberosity below crest in mid-line.
4. a depression for the nuchal musculature on either side of the median ridge	4. depressions indistinct.

The supraoccipital is excluded from the dorsal margin of the foramen magnum by the exoccipitals, and only a narrow arm of the supraoccipital meets the squamosal.

The sutures between the supraoccipital and the exoccipitals are not visible, but their approximate positions are indicated by a difference in bone structure (a change from the dense bone of the supraoccipital to the slightly cancellous bone of the exoccipitals) (see Plate 7). Each exoccipital extends laterad to make contact with the post-tympanic process of the squamosal; however, the dorsolateral part of the exoccipital is separated from the squamosal by an irregular fonticulus that is occupied by the mastoid. Ventrally, the exoccipitals bear the occipital condyles and the paroccipital processes. The condyles have a broad articulating surface dorsally, but this narrows ventrally until the ends of the condyles are c.3.3cm apart, separated by the basioccipital. The condyles are more markedly curved vertically than transversely. The hypoglossal foramen passes ventrolaterad between the condyle and the paroccipital process, and on both sides of M19100a there is a smaller nutrient foramen just anterior to the hypoglossal (see Plate 8). The paroccipital processes are directed ventrad and their apices are extended beyond the occipital condyles; they are triangular in shape and are flattened anteroposteriorly.

The foramen magnum is large and is completely surrounded by the exoccipitals except for the area between the ventral ends of the condyles where the basioccipital intrudes.

The basioccipital is an indistinct bone, whose sutures are obscured,

PLATE 7

Libysiren sickenbergi gen. et sp. nov.
M19100a: occipital region

FIGURE 10

Drawing of Plate 7

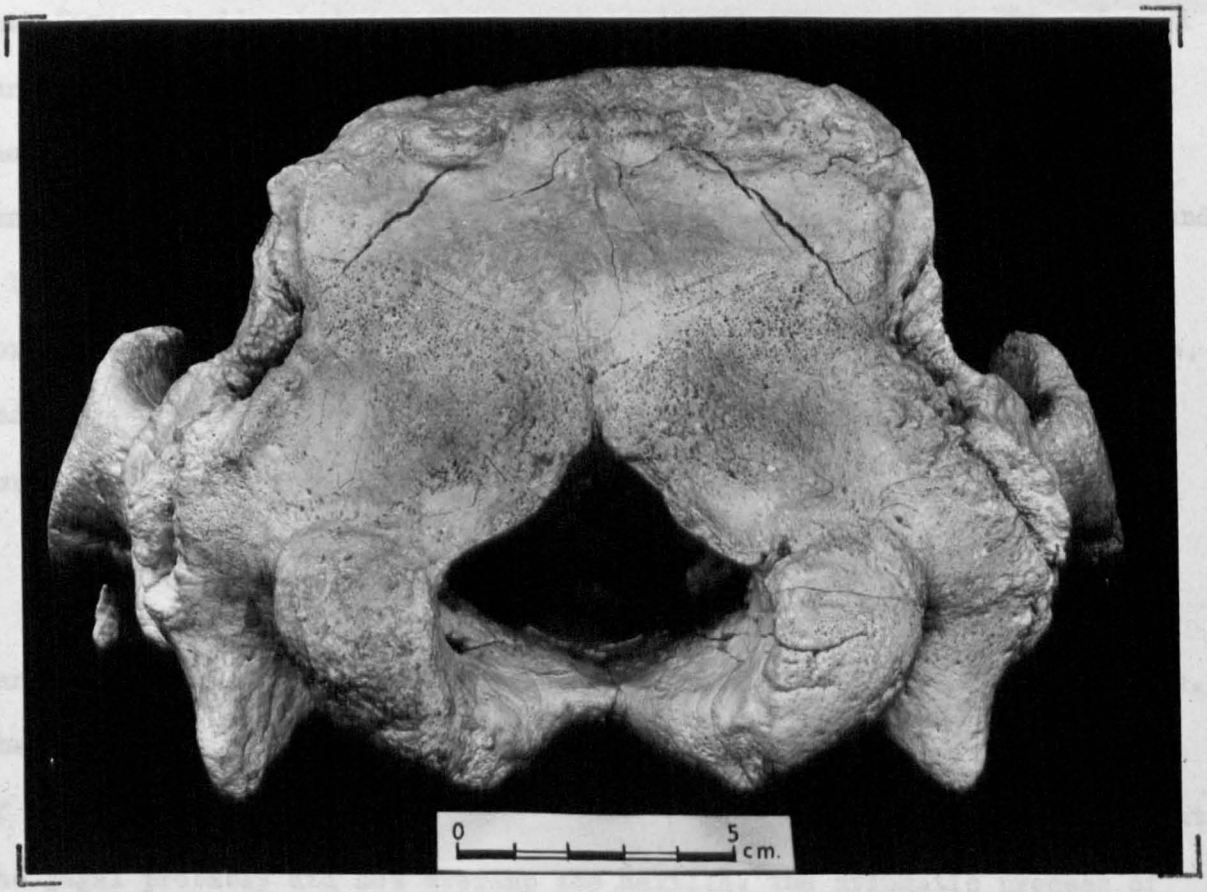
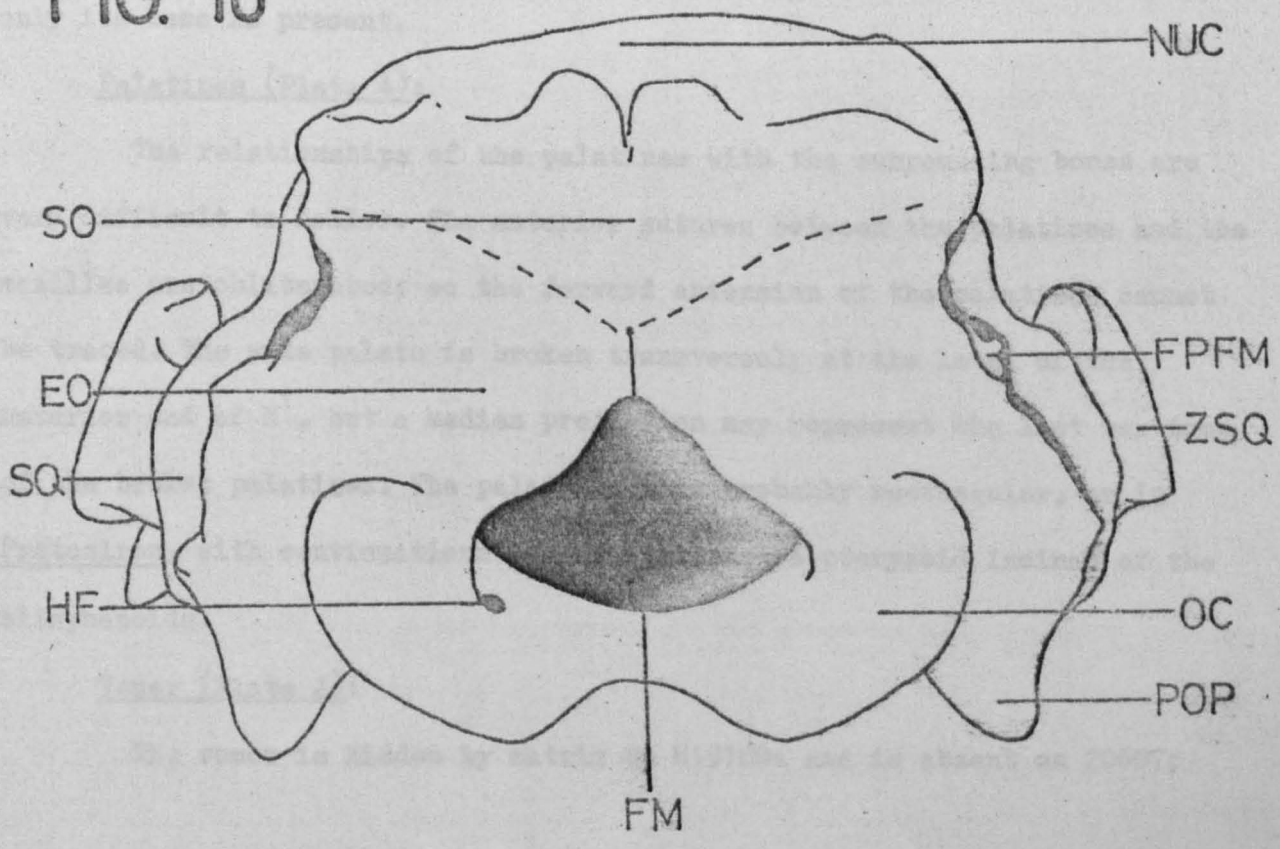


FIG. 10



that forms a bridge between the exoccipitals and the sphenoid. The external surface of the basioccipital bears two raised areas for the attachment of the rectus capitis muscles; the internal surface of the bone is slightly concave. The basioccipital, alisphenoid, squamosal, and exoccipital surround a large ventral opening, the foramen lacerum (formed by the fusion of the foramen lacerum anterius, the foramen lacerum posterius, the foramen ovale, and the stylomastoid foramen). This opening is partially filled by the periotic (see Plate 8).

Jugal (Plates 1, 4, and 6):

The jugal is only present on the left side of M19100a. It forms part of the floor of the orbit and the anterior part of the zygomatic arch. The maxillo-jugal suture cannot be traced with certainty, but the absence of the jugal on the right side has produced a vertical surface showing that the jugal probably did not overlap the maxilla. The zygomatic process of the jugal is laterally compressed and is distinct from the maxillary part. It forms about half of the complete zygomatic arch, and the surface that articulates with the zygomatic process of the squamosal faces posterodorsad. There is some indication of a dorsal postorbital process on the jugal, but only its base is present.

Palatines (Plate 4):

The relationships of the palatines with the surrounding bones are very difficult to follow. The anterior sutures between the palatines and the maxillae are obliterated; so the forward extension of the palatines cannot be traced. The wide palate is broken transversely at the level of the anterior end of M^1, but a median projection may represent the last vestiges of the broken palatines. The palatines were probably rectangular, as in Protosiren, with continuations as far back as the pterygoid laminae of the alisphenoids.

Vomer (Plate 2):

The vomer is hidden by matrix on M19100a and is absent on 20607;

however, it is present in a broken stateon 20608. It is an elongate bone resting on the internal surface of the maxillae. The area of the vomer in contact with the maxillae decreases posteriorly because the bone narrows. The lateral edges of the vomer are vertical, thus forming a deep trough that would normally be occupied by the mesethmoid.

Sphenoid (Plates 1, 8, and 9):

The various parts of the sphenoid cannot be clearly separated on M19100a. The anterior region of this bone complex (the presphenoid and the orbitosphenoids) is intact, but the sutures between the various bones are not visible in most areas. The presphenoid forms a prominent median keel within the nasopharyngeal fossa, but its connections with the orbitosphenoids and the basisphenoid are not apparent. The orbitosphenoids are present, but their areal extent is not discernible due to the absence of definite sutures. There is no indication of sutures between the orbitosphenoid and the adjacent fronto-palatine region, but the suture between the former and the alisphenoid is very prominent and is marked in M19100a by the presence of two foramina.

The posterior region of the complex comprises the basisphenoid and the alisphenoids. The basisphenoid is a thick bone that forms a rigid strut between the presphenoid and the basioccipital as well as connecting the two pterygoid processes. On its internal surface,the basisphenoid exhibits a prominent sella turcica for the pituitary gland. The sutures separating the alisphenoid from the squamosal, parietal, frontal, and orbitosphenoid are visible and can be traced for much of their length. Ventrally, the alisphenoid-squamosal suture can be followed from just anterior to the petrotympanic, where it passes anteriorly and then turns through over 90° to delineate the anterior border of the squamosal. The suture then turns anteriorly again to meet a narrow extension of the parietal; a slight antero-ventral inclination brings the alisphenoid into contact with the frontal and orbitosphenoid. The alisphenoid forms the lateral wall of the dorsal of the

PLATE 8

Libysiren sickenbergi gen. et sp. nov.

M19100a: ear region

FIGURE 11

Drawing of Plate 8

PLATE 8

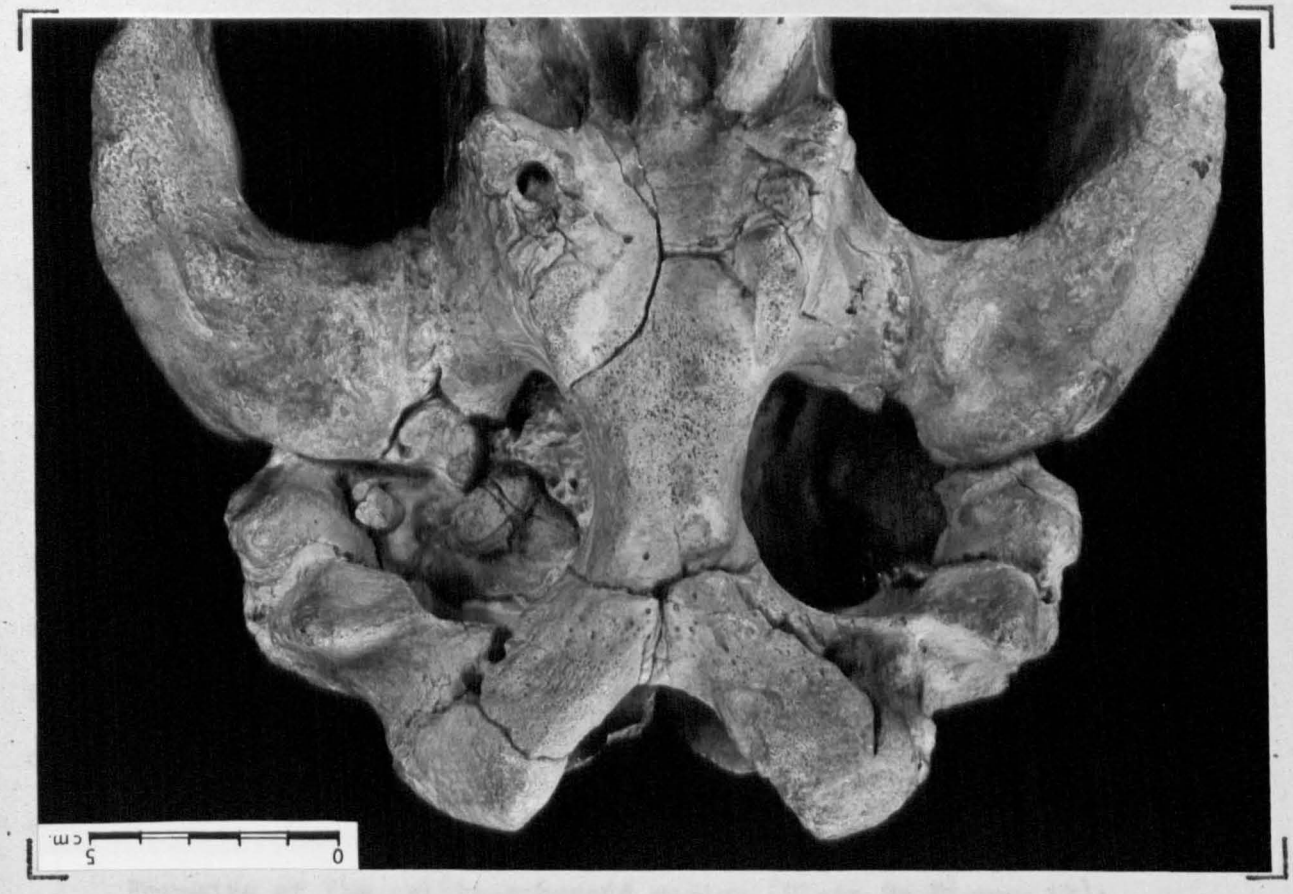
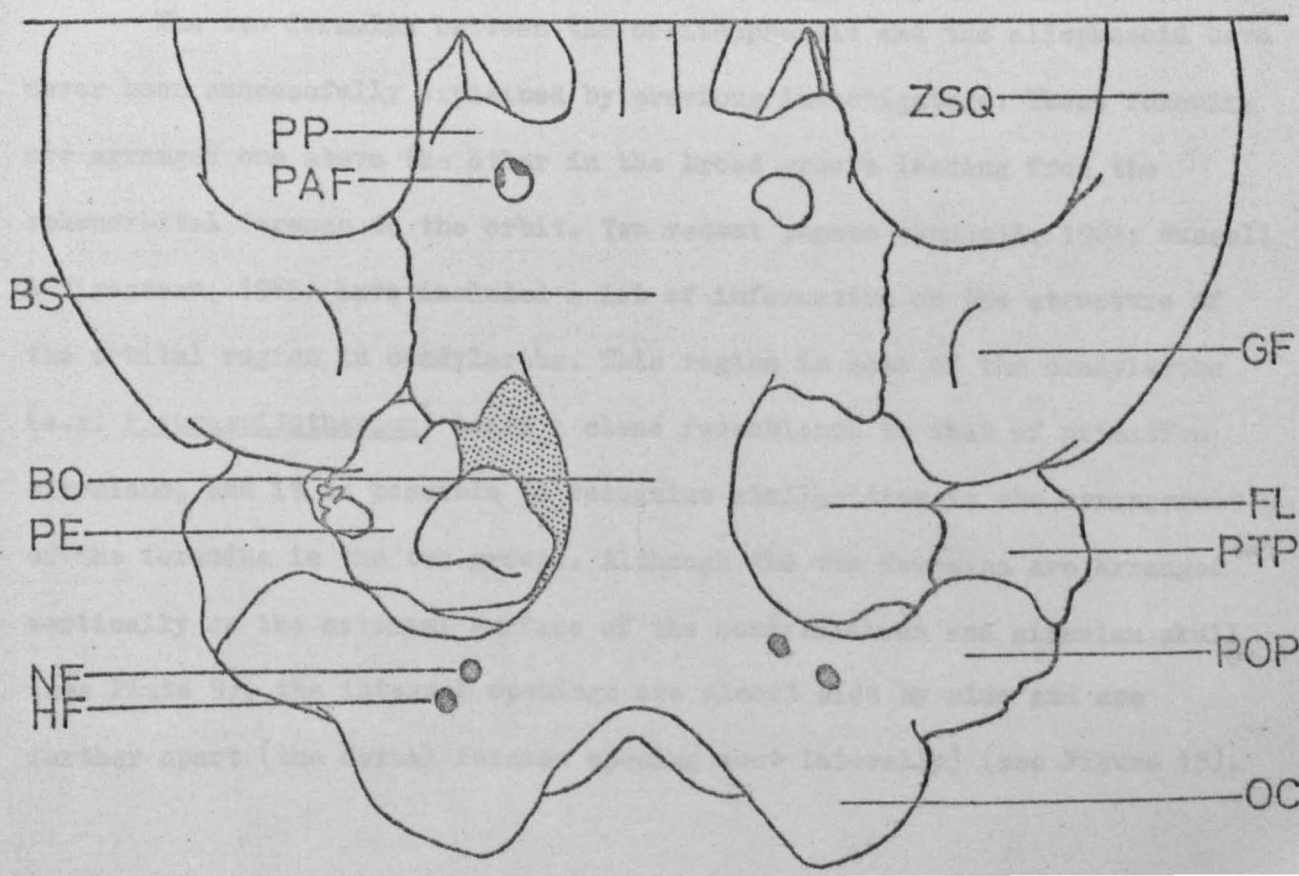


FIG. 11



two previously-mentioned foramina, and then the suture turns sharply posteriorly to pass through the large sphenorbital foramen at the base of the pterygoid process. The last part of the suture, within the sphenorbital canal, cannot be traced. (See Plate 8).

A very prominent pterygoid process is present on each side of the basisphenoid, but it is impossible to say exactly which bones contribute towards to its construction since no sutures are visible. The lateral wall appears to consist largely of an alisphenoid lamina, whereas the medial wall is essentially basisphenoid. A large part of each process is missing and only their stout bases are preserved. The broken ventral surface is anteroposteriorly elongated and narrows caudally. The anterior face of each pterygoid process is occupied by three openings - a large dorsal sphenorbital foramen and the two anterior foramina of the alisphenoid canal.

Foramina of the orbito-sphenoid region (Plate 9; Figure 13):

The ethmoidal foramen is very small and is situated in the lateral wall of the frontal above M^3. Although the foramen itself is small it is made more apparent by a distinct groove running forwards towards the orbit.

The two foramina between the orbitosphenoid and the alisphenoid have never been successfully explained by previous investigators. These foramina are arranged one above the other in the broad groove leading from the sphenorbital foramen to the orbit. Two recent papers (Russell, 1964; Russell & Sigogneau, 1965) have included a lot of information on the structure of the orbital region in condylarths. This region in some of the condylarths (e.g. Pleuraspidotherium) bears a close resemblance to that of primitive sirenians, and it is possible to recognize similarities in the arrangement of the foramina in the two groups. Although the two foramina are arranged vertically on the external surface of the condylarthran and sirenian skull (see Plate 9), the internal openings are almost side by side and are further apart (the dorsal foramen opening most laterally) (see Figure 13).

PLATE 9

Libysiren sickenbergi gen. et sp. nov.

M19100a : sphenoid foramina

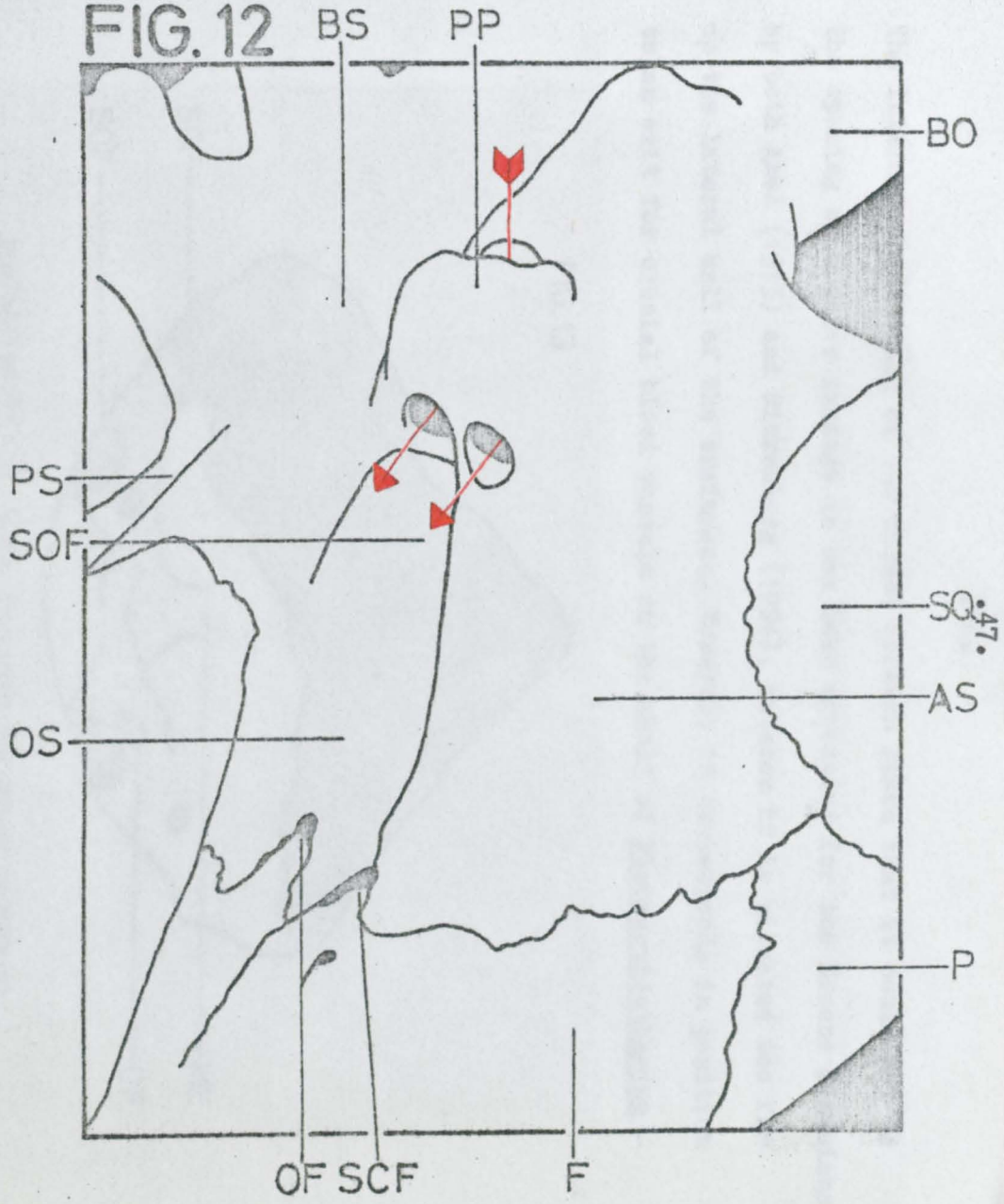
x1.5

FIGURE 12

Drawing of Plate 9

PLATE 9

FIG. 12



The internal positioning of the dorsal foramen shows that it could not be the opening of a nerve passage as has been advocated for the Eocene sirenians by both Abel (1913) and Sickenberg (1934), because it is situated too far up the lateral wall of the braincase. However, it corresponds in position to an exit for cranial blood vessels on the skull of Pleuraspidotherium - the sinus canal foramen.

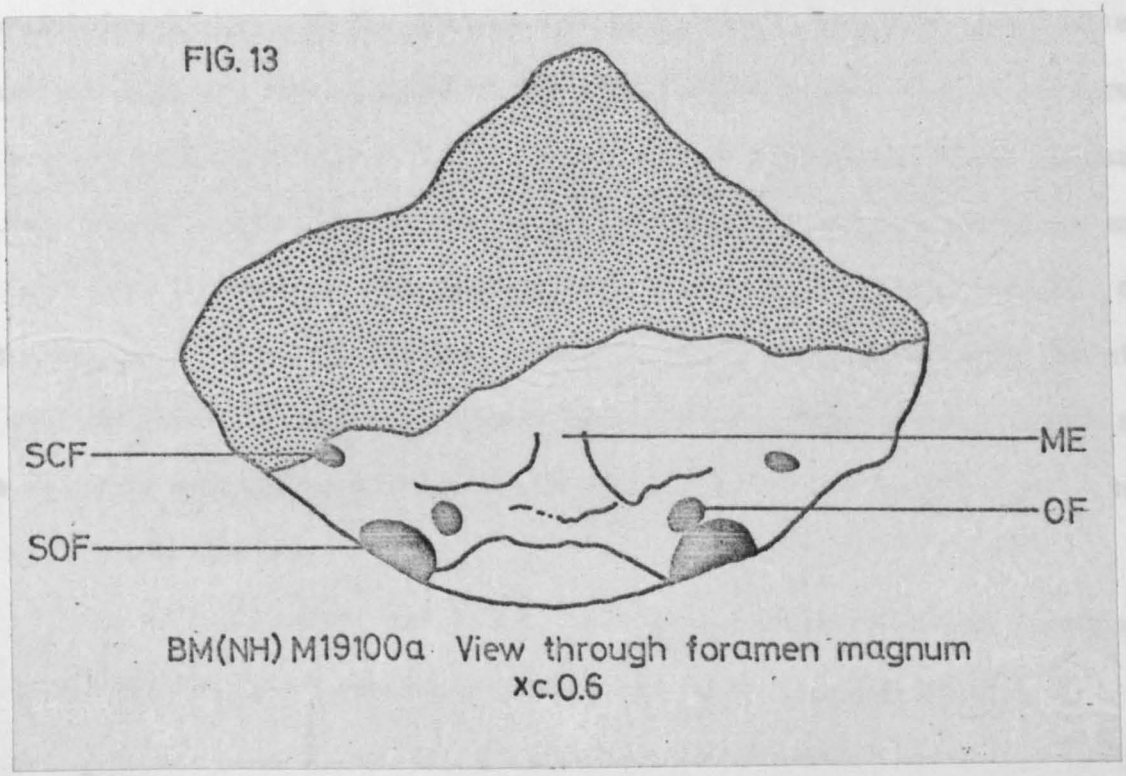


TABLE 3

	Abel (1913)	Sickenberg (1934)	Present Author
dorsal foramen	foramen rotundum	ethmoidal foramen	sinus canal foramen
ventral foramen	optic foramen	optic foramen	optic foramen

The large sphenorbital foramen lies at the base of the pterygoid process and is the anterior opening of the sphenorbital canal. As in Pleuraspidotherium, the foramen rotundum is not a separate opening and its branch of the trigeminal nerve leaves the braincase via the sphenorbital canal.

Two smaller foramina below the sphenorbital foramen join within the pterygoid process and emerge on its ventral surface as a large single foramen (the relationship between these three foramina is indicated by the arrow on

Figure 12). This situation is comparable to that seen in Protosiren, where the alisphenoid canal penetrates the posterior surface of the pterygoid process in a dorsal direction and then divides into two smaller canals before emerging at the anterior surface of the process. The ventral position of the single foramen on M19100a is the result of the pterygoid process being broken; if the process had been intact the canal would have opened posteriorly. The alisphenoid canal undoubtedly served as a passage for the internal maxillary artery, but the two branches into which the artery divides cannot be identified with certainty. The two anterior openings are not identical in size, and it is most probable that the larger (medial) one contained the direct continuation of the internal maxillary artery whilst the smaller (lateral) one contained a minor branch. This lateral branch may have been the mandibular artery, which would have turned ventrad and entered the mandibular foramen.

The cranial nerves and blood vessels passing through the foramina and canals of the orbito-sphenoid region can be summarized thus:

Nerves	
optic foramen	II
sphenorbital canal (incl. foramen rotundum)	III, IV, V_1 pars, V_2, VI
ethmoidal foramen	V_1 pars
Blood Vessels	
sinus canal foramen	superior ophthalmic vein, meningeal veins, middle meningeal artery
alisphenoid canal	internal maxillary artery

Squamosal (Plates 1, 6, 7, and 11):

The squamosal is a large bone forming the postero[illegible] wall of the braincase and the posterior half of the zygomatic arch. Dorsally, this bone makes contact with the parietal as far back as the nuchal crest; anteriorly and ventrally it meets the sphenoid; posteriorly, there is an open suture

with the exoccipital. The main part of the squamosal (that forming the posterolateral wall of the braincase) gives rise to two processes - a lateral zygomatic process and a ventral post-tympanic process.

The zygomatic process emerges from the side of the cranium at right angles to its lateral wall, and this lateral extension bears the glenoid fossa on its ventral surface. The glenoid area is broad anteroposteriorly and the fossa is a shallow, concave area with its deepest part situated medially. In front of the fossa there is a short, transverse ridge that is most prominent on the anterolateral corner of the articulation. A low post-glenoid process forms the posterior margin of the fossa. Lateral to the glenoid region, the zygomatic process of the squamosal turns forwards and forms the posterior part of the zygomatic arch. This part of the arch is laterally compressed and high.

The postglenoid process is separated from the post-tympanic process by a deep superficies meatus. This passage is well exposed on both sides of M19100a, and in 20607 a short length (c.3.4cm) of the soft tissue of the external auditory meatus is preserved. The external auditory meatus passes laterad along the passage and then extends dorsad for a short distance on the outside of the skull. The superficies meatus is fully open ventrally.

The post-tympanic process extends posteroventrad from the squamosal proper to meet the exoccipital. The dorsal edge of this process forms the ventral boundary of the fonticulus mastoideus and there is a prominent ridge running diagonally across the process from the anterior rim of the fonticulus to the tip of the process.

Ethmoidalia (Plates 10 and 11):

The ethmoid region of M19100a cannot be seen because the nasal cavity is full of matrix, but in 20607 the posterior part of this region is present and clearly visible. Medial to the lacrimal, the internal surface of each nasal is expanded inwards as a bulbous enlargement, and these two expansions constrict the nasal passage. The ethmoid is situated below the anterior end

PLATE 10

Libysiren sickenbergi gen. et sp. nov.

UB20607: ethmoidalia

FIGURE 14

Drawing of Plate 10

PLATE 10

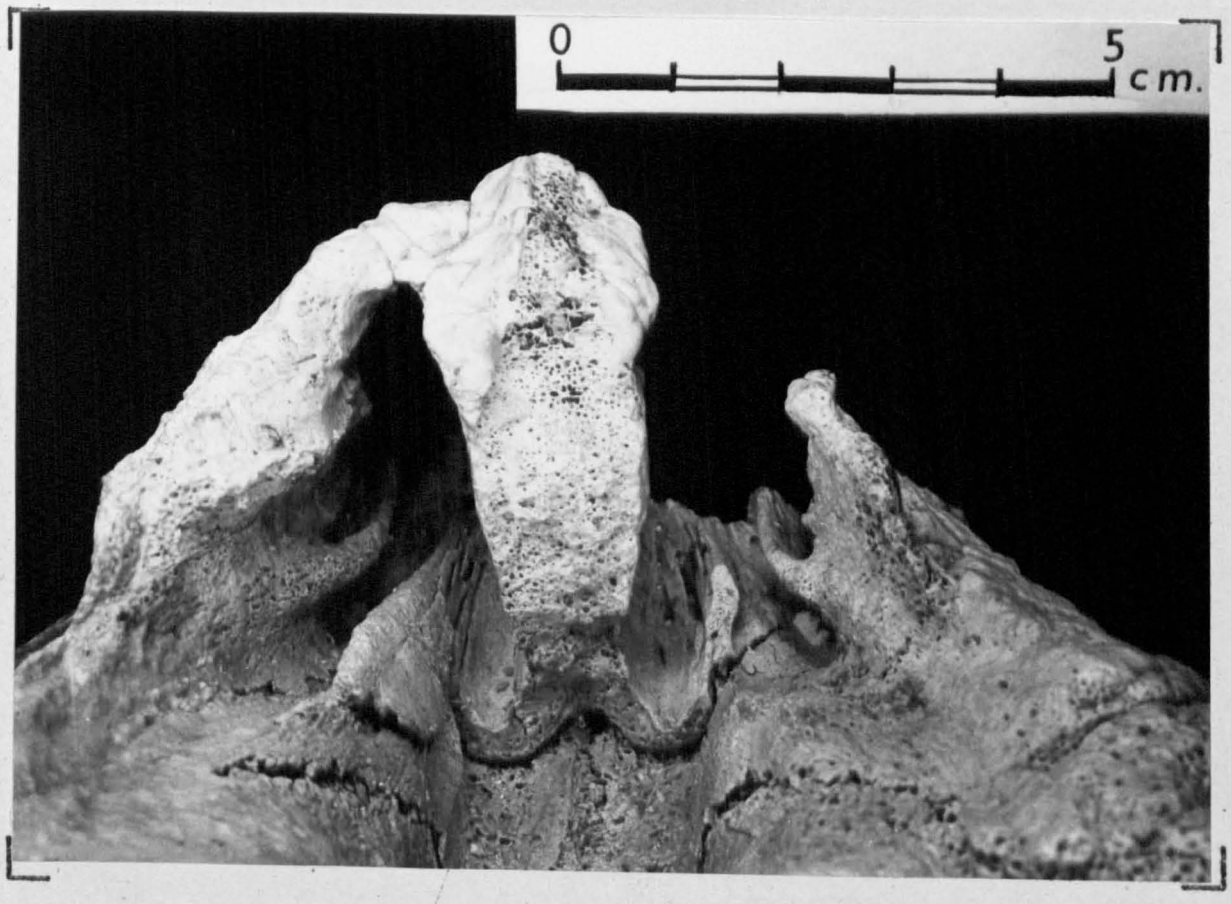


FIG. 14

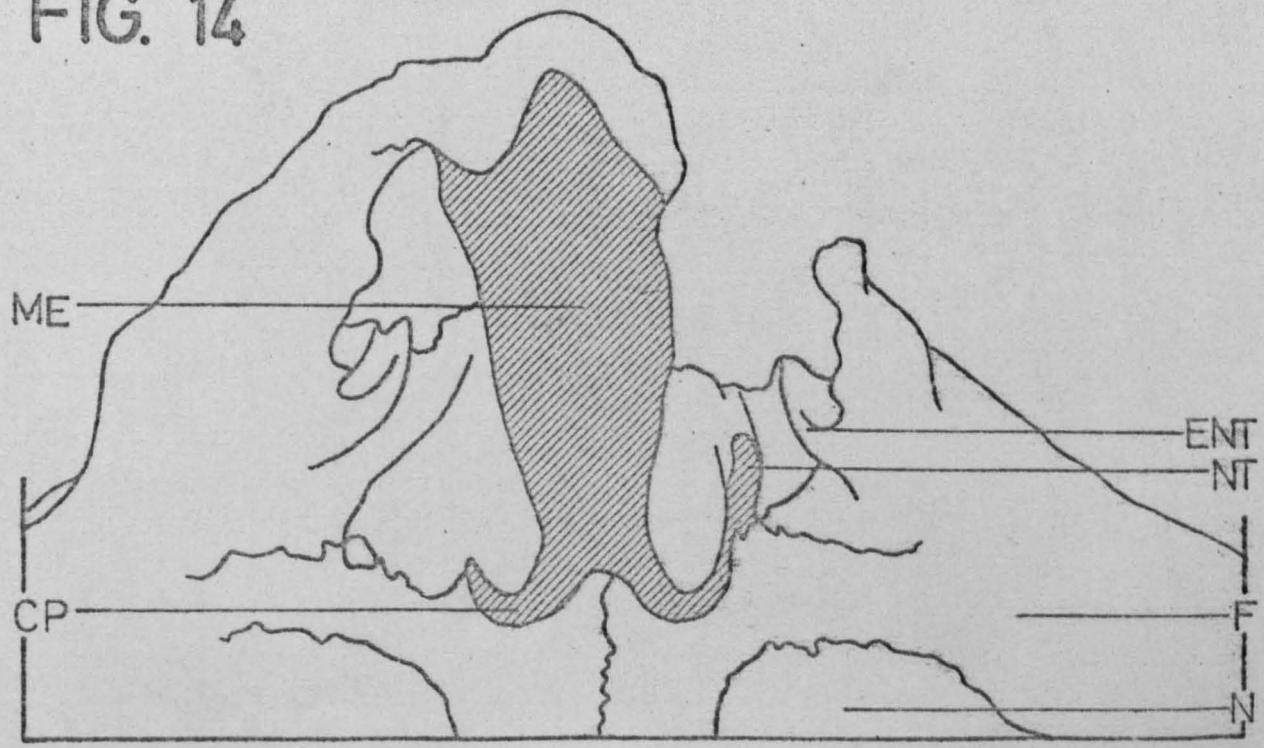


PLATE 11

Libycaiman sickenbergi gen. et sp. nov.

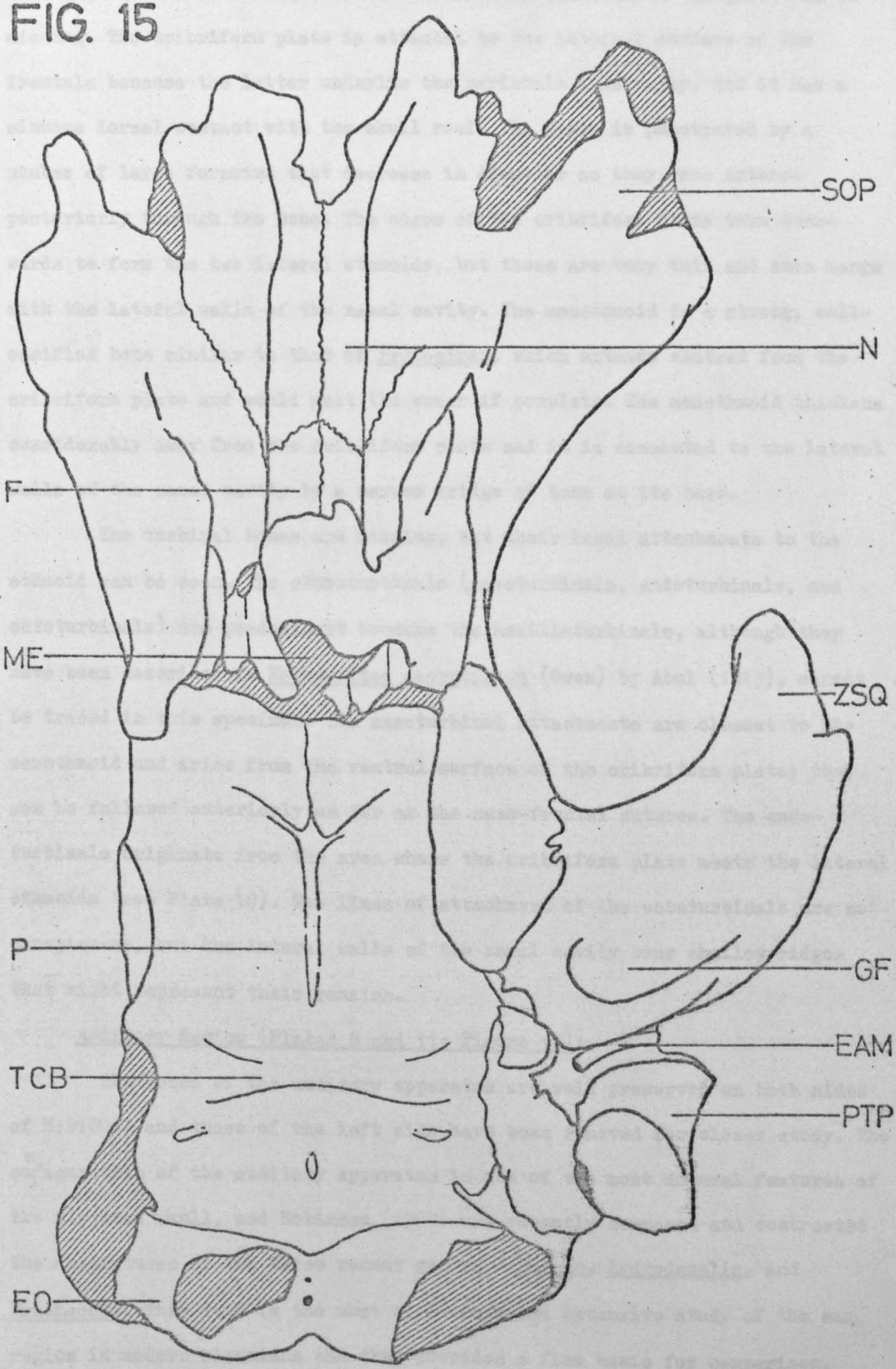
UB20607: ventral view of skull roof

FIGURE 15

Drawing of Plate 11

PLATE 11

FIG. 15



of the parietals in 20607, but most of the bone anterior to the parietals is missing. The cribriform plate is attached to the internal surface of the frontals because the latter underlie the parietals internally, and it has a sinuous dorsal contact with the skull roof. The plate is penetrated by a number of large foramina that decrease in diameter as they pass antero-posteriorly through the bone. The edges of the cribriform plate turn downwards to form the two lateral ethmoids, but these are very thin and soon merge with the lateral walls of the nasal cavity. The mesethmoid is a strong, well-ossified bone similar to that of Protosiren, which extends ventrad from the cribriform plate and would meet the vomer if complete. The mesethmoid thickens considerably away from the cribriform plate and it is connected to the lateral walls of the nasal cavity by a narrow bridge of bone at its base.

The turbinal bones are missing, but their basal attachments to the ethmoid can be seen. The ethmoturbinals (nasoturbinals, endoturbinals, and ectoturbinals) are predominant because the marilloturbinals, although they have been described in Eotheroides aegyptiacum (Owen) by Abel (1913), cannot be traced in this specimen. The nasoturbinal attachments are closest to the mesethmoid and arise from the ventral surface of the cribriform plate; they can be followed anteriorly as far as the naso-frontal sutures. The endoturbinals originate from the area where the cribriform plate meets the lateral ethmoids (see Plate 10). The lines of attachment of the ectoturbinals are not conspicuous, but the lateral walls of the nasal cavity bear shallow ridges that might represent their remains.

Auditory Region (Plates 8 and 11; Figure 16):

The bones of the auditory apparatus are well preserved on both sides of M19100a, and those of the left side have been removed for closer study. The configuration of the auditory apparatus is one of the most unusual features of the sirenian skull, and Robineau (1969) has recently compared and contrasted the apparatuses of the three recent genera - Dugong, Hydrodamalis, and Trichechus. This work is the most up-to-date and extensive study of the ear region in modern sirenians and thus provides a firm basis for comparison.

Abel (1913) described the ear region of Eotheroides aegyptiacum and then Sickenberg (1934) did the same for Protosiren fraasi Abel and Prototherium veronense de Zigno, but both of these accounts are confusing because at that time there was no standardized nomenclature and neither author gave sufficiently clear illustrations.

Robineau (1969) divided the sirenian periotic into the pars petrosa, the tegmen tympani, and the pars mastoidea. The tegmen tympani and pars mastoidea of the Dugong periotic fit into corresponding depressions on the internal surface of the squamosal, but in M19100a only the tegmen tympani has such a close contact with the squamosal. The pars mastoidea of M19100a only touches the squamosal on its extreme posterolateral edge.

The pars petrosa is a very robust structure with rounded edges, and its external surface is almost identical to that of Dugong - the promontorium, fenestra cochleae, fenestra vestibuli, and foramen endolymphaticum occupy very similar positions in the two genera. However, the internal surface of the pars petrosa shows a number of features that differ between the two genera. In M19100a the path of the auditory nerve (VIII) is horizontal from the anterior edge of the pars petrosa to the foramen acusticum inferius, and the groove that contained the nerve is not very deep. The facial foramen is small and has a narrow suprafacial commissure above. The right pars petrosa of M19100a has been broken to expose the cochlea, which has just over 1.5 turns.

The tegmen tympani is separated from the pars mastoidea by a very faint groove. The tegmen is formed of very dense bone and has a pronounced anterior process that bears an attachment surface for the anterior arm of the tympanic ring. A narrow nutrient foramen penetrates the anterior third of the tegmen.

The pars mastoidea projects beyond the posterior edge of the tegmen tympani as a large facies petrosi fonticuli mastoidei, but the latter does not protrude beyond the fonticulus mastoideus. Anterolaterally, the pars mastoidea bears a large flattened process for the attachment of the posterior arm of the tympanic ring.

FIGURE 16

Libysiren sickenbergi gen. et sp. nov.

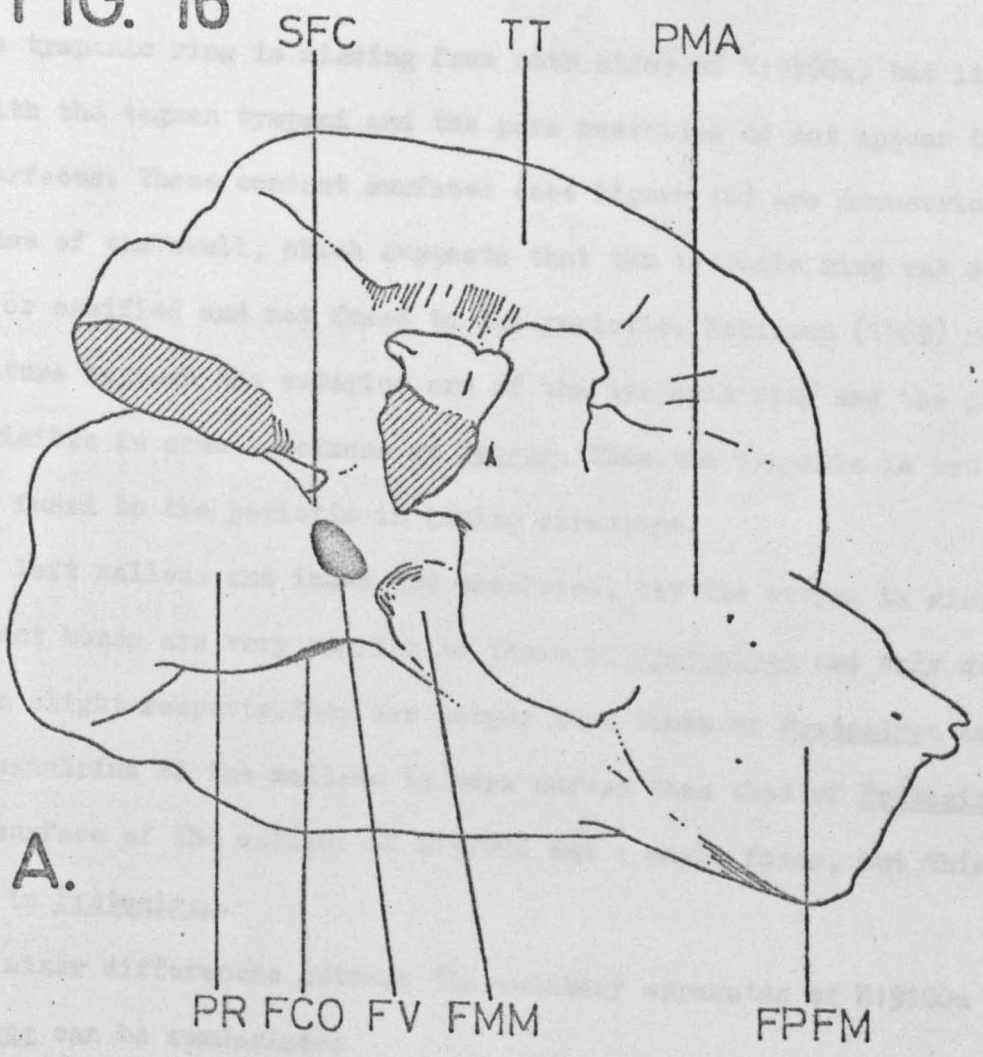
M19100a

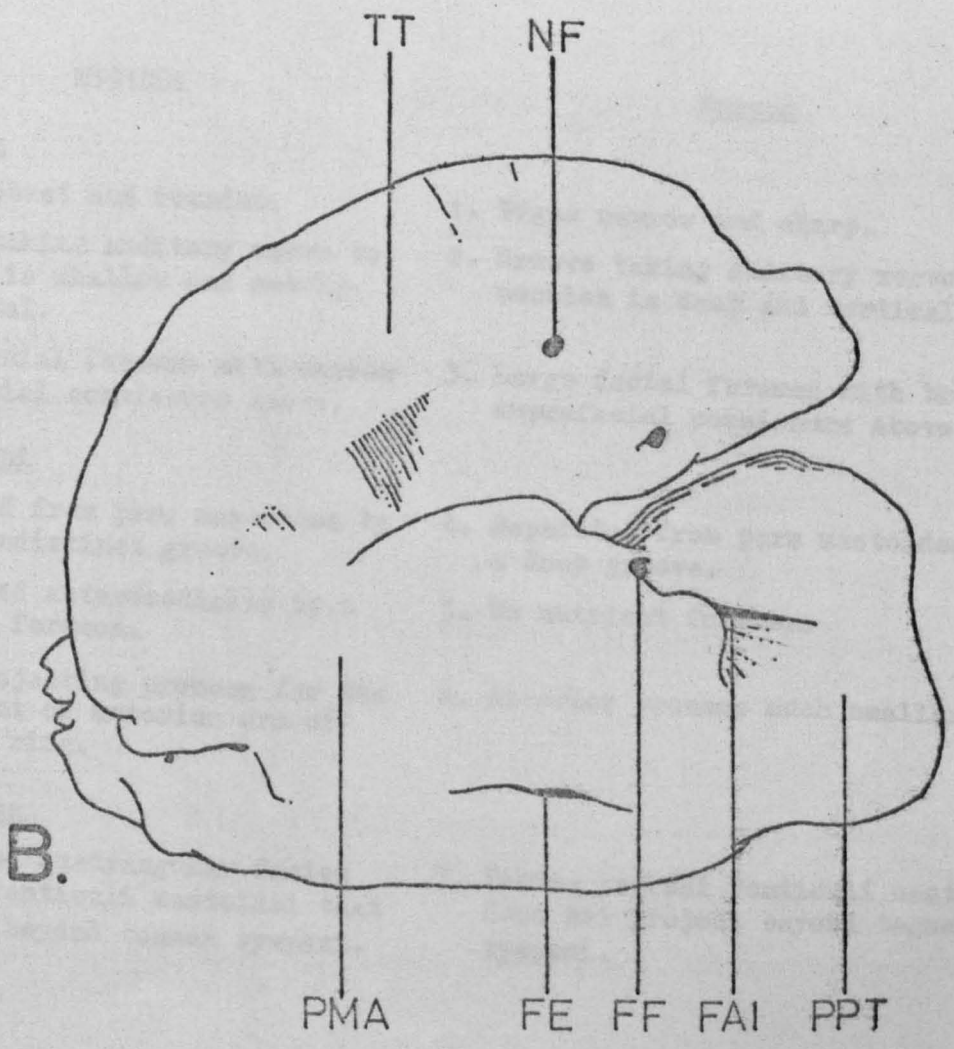
A : lateral view of petrotympanic

B : medial view of petrotympanic

x2

FIG. 16





The tympanic ring is missing from both sides of M19100a, but its contacts with the tegmen tympani and the pars mastoidea do not appear to be fracture surfaces. These contact surfaces (see Figure 16) are symmetrical on both sides of the skull, which suggests that the tympanic ring was either unossified or ossified and not fused to the periotic. Robineau (1969) noticed that the suture between the anterior arm of the tympanic ring and the periotic was still visible in some specimens of Dugong. Thus the tympanic is not necessarily fused to the periotic in living sirenians.

The left malleus and incus are preserved, but the stapes is missing. The two intact bones are very similar to those of Protosiren and only differ from them in slight respects.They are larger than those of Protosiren and the crista manubrium of the malleus is more curved than that of Protosiren. The dorsal surface of the malleus of M19100a has a small fossa, but this is not visible in Protosiren.

The minor differences between the auditory apparatus of M19100a and that of Dugong can be summarized:

TABLE 4

M19100a	Dugong
Pars petrosa	
1. Edges robust and rounded.	1. Edges narrow and sharp.
2. Groove taking auditory nerve to cochlea is shallow and nearly horizontal.	2. Groove taking auditory nerve to cochlea is deep and vertical.
3. Small facial foramen with narrow suprafacial commissure above.	3. Large facial foramen with broad suprafacial commissure above.
Tegmen tympani	
4. Separated from pars mastoidea by a very indistinct groove.	4. Separated from pars mastoidea by a deep groove.
5. Penetrated anteromedially by a nutrient foramen.	5. No nutrient foramen.
6. Large projecting process for the attachment of anterior arm of tympanic ring.	6. Anterior process much smaller.
Pars mastoidea	
7. Has large, quadrangular facies petrosi fonticuli mastoidei that projects beyond tegmen tympani.	7. Facies petrosi fonticuli mastoidei does not project beyond tegmen tympani.

TABLE 4 (cont.)

	M19100a	Dugong
Tympanic		
8.	Not fused to periotic.	8. Usually fused to periotic.
Ossicles		
9.	Crista manubrium not produced into a manubrium mallei.	9. Crista manubrium forms a prominent manubrium mallei.
10.	Malleus fused to incus, but not fused to tympanic; incus fused to periotic by processus brevis.*	10. Malleus not fused to incus, but fused to tympanic; incus fused to periotic by processus brevis.*

* Because the ossicular chain of Libysiren is only fused to the petrotympanic at one point it has more freedom of movement than the ossicular chain of Dugong, which is fused to the petrotympanic at two points. The oscillation of the chain in Dugong has been measured up to 17kHz, but the damping produced by the two attachments limits the resonance to between 2kHz and 4kHz (Fleischer, 1971). The hearing range of Libysiren could be expected to be greater than that of Dugong because the damping of the ossicles is not so marked.

Cranial cavity and endocranial cast (Plate 11):

The basicranium is missing from 20607 and this makes it possible to see the internal structure of the roof of the cranium. A latex endocranial cast gives some idea of the size and shape of the brain, but previous authors (Owen, 1875; Edinger, 1939; Hill, 1945) have noted that there is no close relationship between the brain of sirenians and the surrounding cranial cavity due to the presence of a thick, vascular dura mater. Since the endocranial cast is not a true representation of the brain I have decided to replace the precise anatomical terms "cerebrum" and "cerebellum" by the less precise topographical terms "cerebral region" and "cerebellar region".

The latex cast shows that the cerebral and cerebellar regions are separated by a transverse groove that is produced by a prominent ridge on the internal surface of the parietals - the ossified tentorium cerebelli. The cerebral hemispheres are likewise separated by a prominent longitudinal ridge on the cast that fits into the depression formed at the junction of the parietals — thus an ossified falx cerebri is absent. Two smaller ridges

diverge anterolaterad from the longitudinal ridge at the level of the anterior edge of the zygomatic process of the squamosal; these are produced by the internal arrangement of the fronto-parietal sutures. The longitudinal ridge decreases in height posteriorly and disappears before it reaches the tentorium groove. Each cerebral hemisphere is divided into a frontal part and a parietal part by an indistinct Sylvian sulcus that passes anteroventrad from just in front of the tentorium groove.

The ossified tentorium is broad and has a small median process on its posterior surface. The small cerebellar region is bisected by a short ridge of bone that is most prominent in the angle between the parietals and the occipital and is at right angles to the tentorium. Two other minor processes of the skull wall make impressions on the lateral edges of the cerebellar region. The posterior surface of the cerebellar region is sharply inclined to the dorsal surface and the corresponding surface of the skull is markedly pitted.

Mandible (Plates 12 and 13; Figure 19):

Six mandibular fragments are known and that of the holotype (M19100b) is the best preserved. The latter consists of the symphysis, the majority of both horizontal rami, and parts of the vertical rami: some features that are absent from this specimen can be seen on one or more of the other fragments (20609, 20610, 20611, 20612, and 20613).

The symphysis is very robust as in all other fossil and living sirenians, and it has a nearly circular sagittal outline. The tooth-bearing surface of the symphysis is inclined at an angle of c.33° to the corresponding surface of the horizontal rami, but on most specimens this region has been so extensively damaged that only the bottoms of the alveoli are present. The internal surface of the symphysis is seen best in 20609 and it is modified to receive the lingual musculature; this modification takes the form of two lateral, oval depressions that are separated by a median groove. The horizontal rami diverge at an angle of c.33° and they are broadest dorsally.

PLATE 12

Libvairan sickenbergi gen. et sp. nov.
M19100b: left lateral view of mandible

FIGURE 17

Drawing of Plate 12

PLATE 12

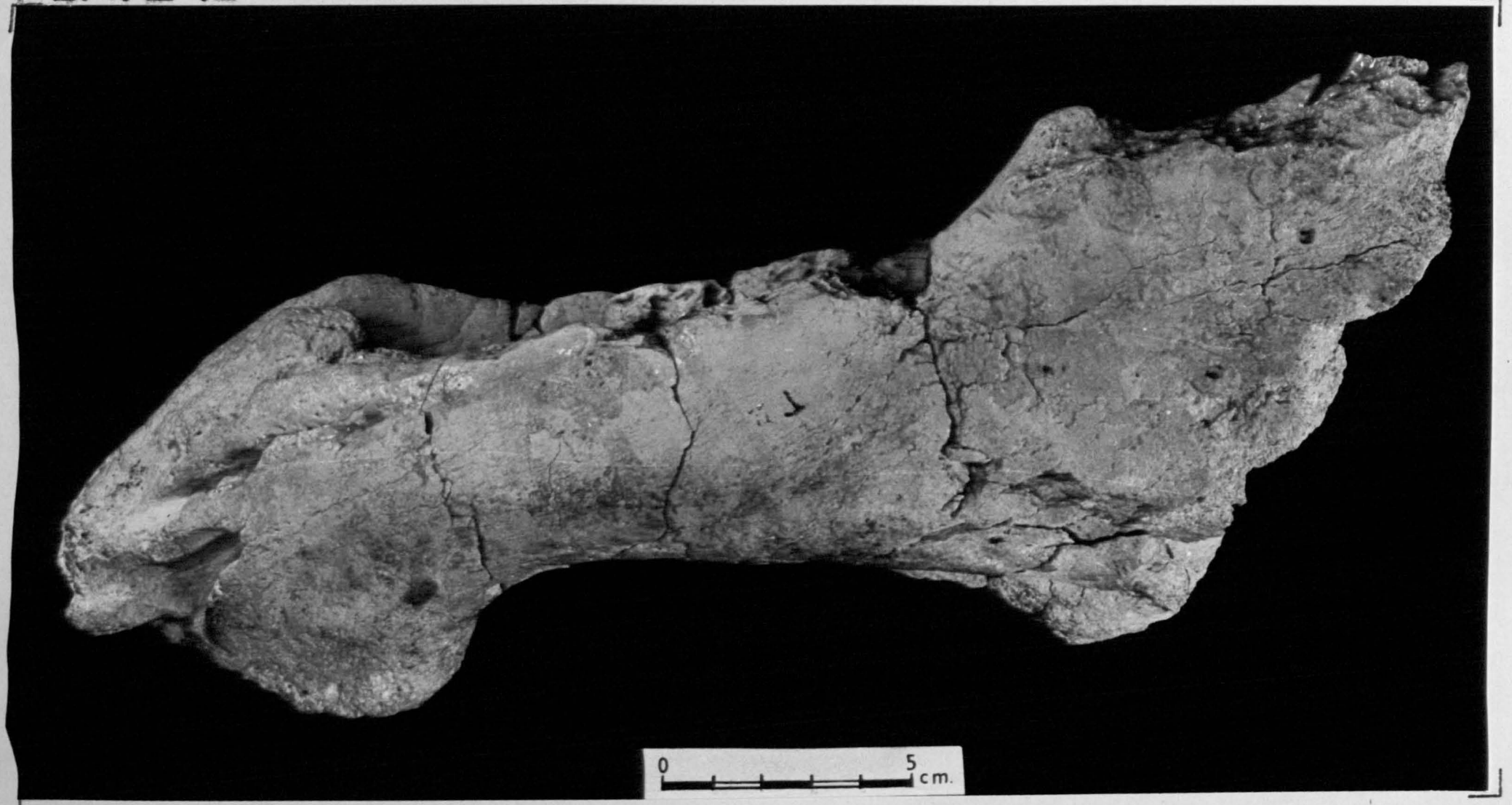


FIG. 17

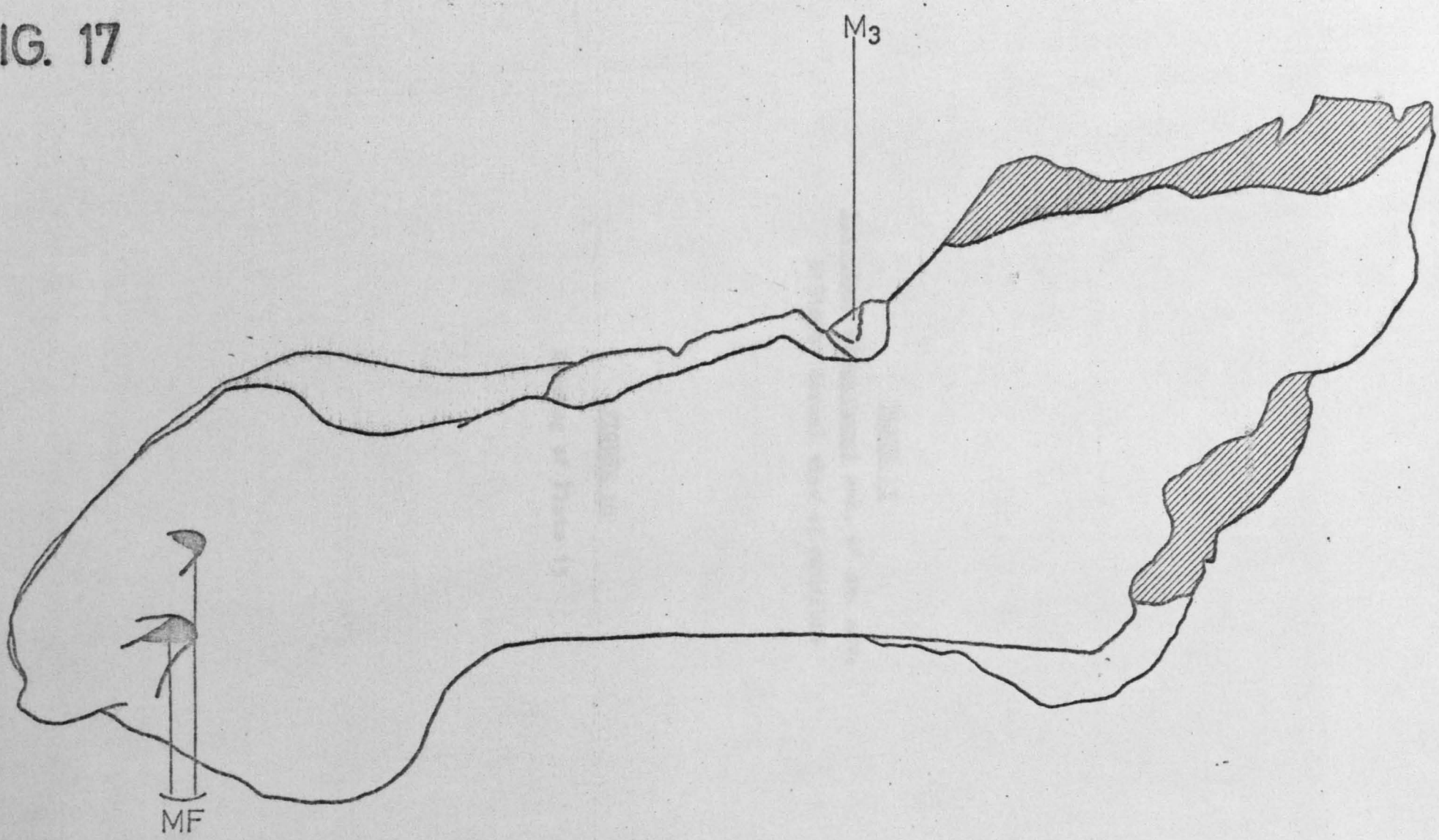


PLATE 13

Libysiran sickenbergi gen. et sp. nov.

M19100b: dorsal view of mandible

FIGURE 18

Drawing of Plate 13

PLATE 13

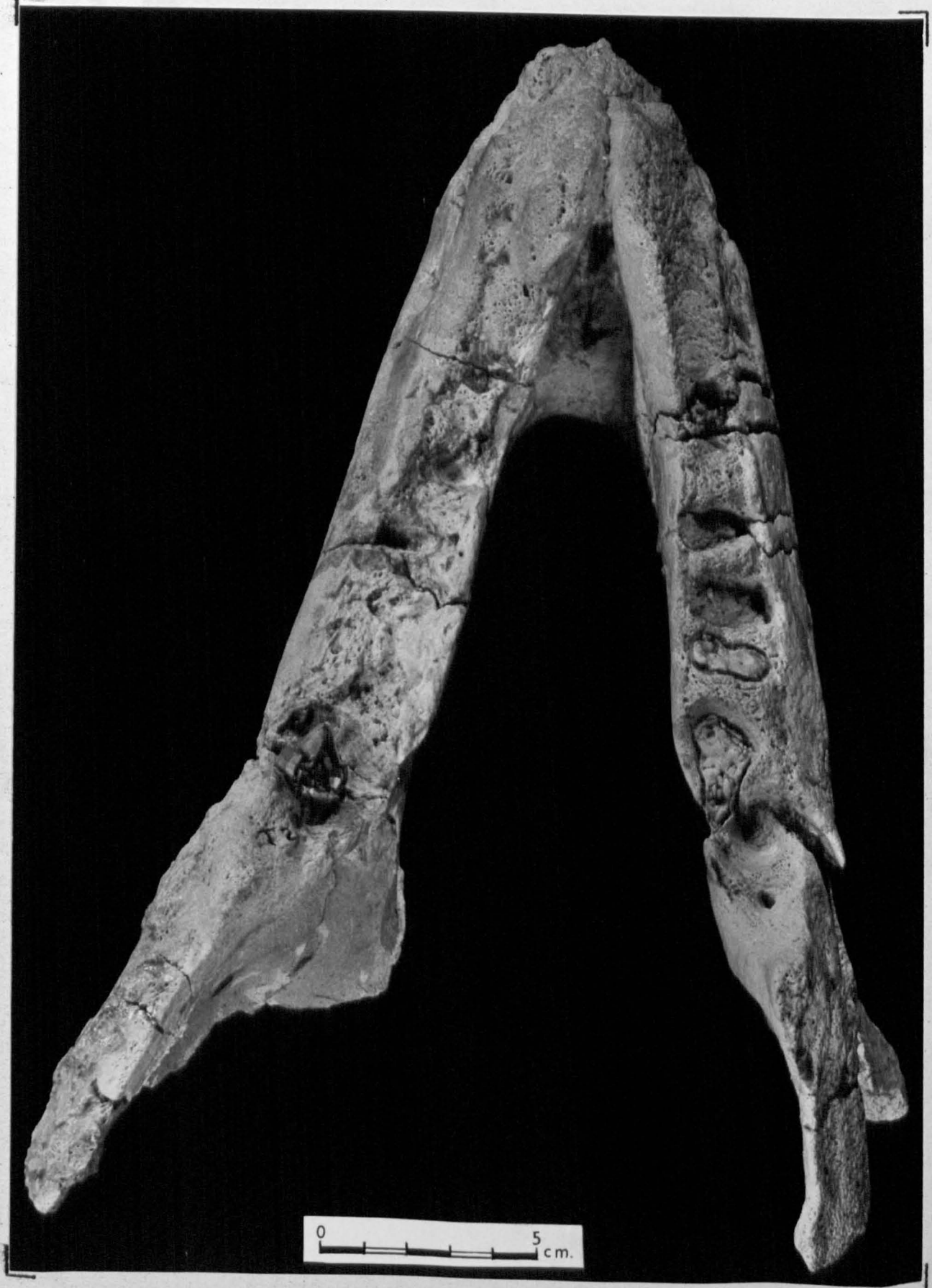
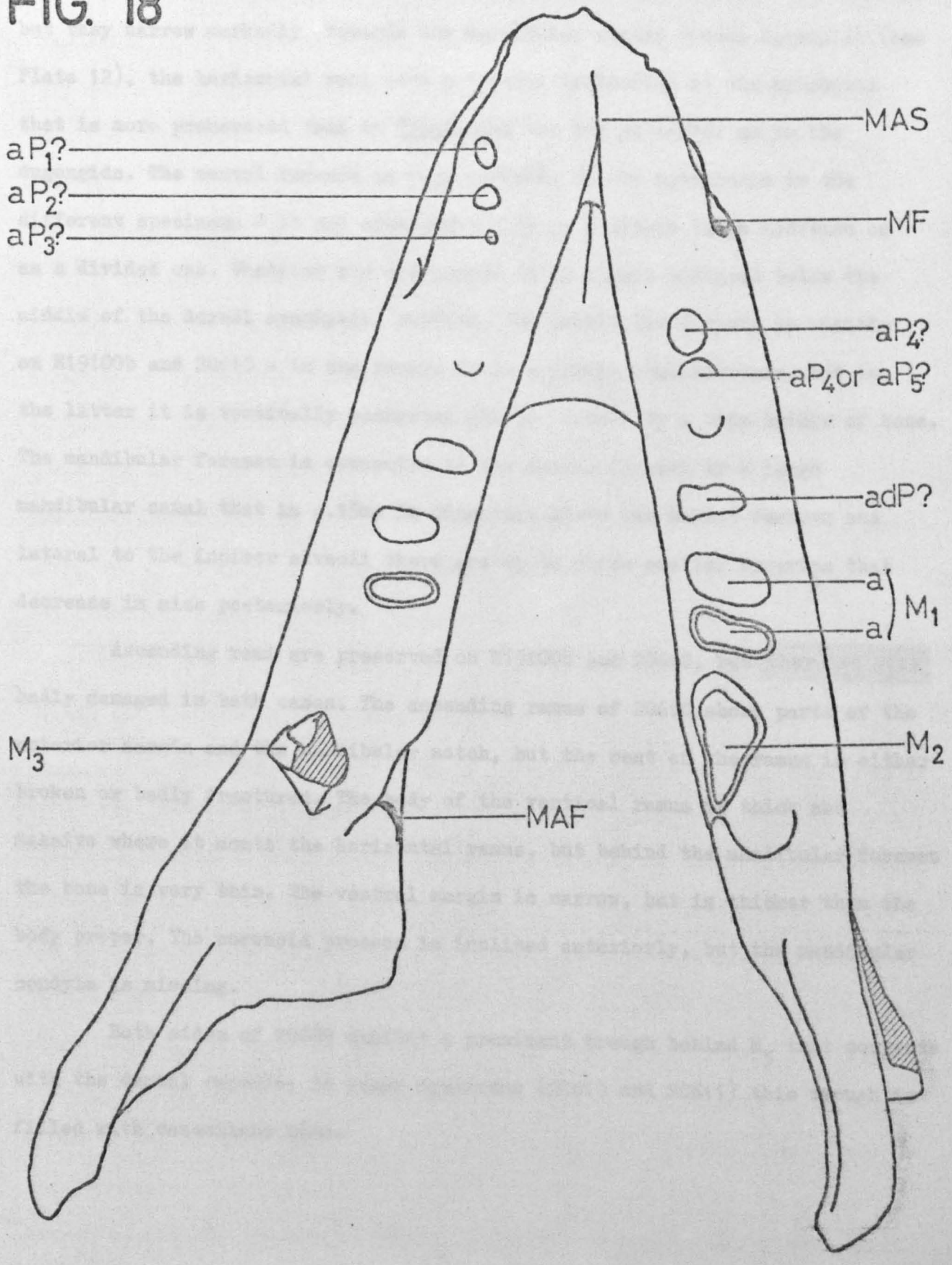


FIG. 18



In all of the specimens, the lingual and labial sides of the alveoli (and the partitions between them) have been broken away so that the rami appear shallower than normal. The ventral surfaces of the rami are broad anteriorly, but they narrow markedly towards the mandibular angle. Viewed laterally (see Plate 12), the horizontal rami have a ventral deflection at the symphysis that is more pronounced than in Trichechus but not so marked as in the dugongids. The mental foramen is very variable in its appearance in the different specimens - it may open externally as a single large aperture or as a divided one. Whatever its appearance it is always situated below the middle of the dorsal symphysial surface. The mandibular foramen is visible on M19100b and 20610 - in the former it is a simple oval aperture, but in the latter it is vertically elongated and is crossed by a thin bridge of bone. The mandibular foramen is connected to the mental foramen by a large mandibular canal that is c.15mm in diameter. Above the mental foramen and lateral to the incisor alveoli there are up to three smaller foramina that decrease in size posteriorly.

Ascending rami are preserved on M19100b and 20610, but they are very badly damaged in both cases. The ascending ramus of 20610 shows parts of the anterior margin and the mandibular notch, but the rest of the ramus is either broken or badly fractured. The body of the vertical ramus is thick and massive where it meets the horizontal ramus, but behind the mandibular foramen the bone is very thin. The ventral margin is narrow, but is thicker than the body proper. The coronoid process is inclined anteriorly, but the mandibular condyle is missing.

Both sides of 20609 exhibit a prominent trough behind M_3 that connects with the dental capsule; in other specimens (20610 and 20611) this trough is filled with cancellous bone.

Dentition

The dentition is only represented by two broken lower molars (20615), but M19100a/b and the several mandible fragments do contain some alveoli from which it is possible to estimate the dental formula. The alveoli are very shallow and are difficult to differentiate because the walls of many of them are absent, but the presence of roots in some helps to simplify this problem.

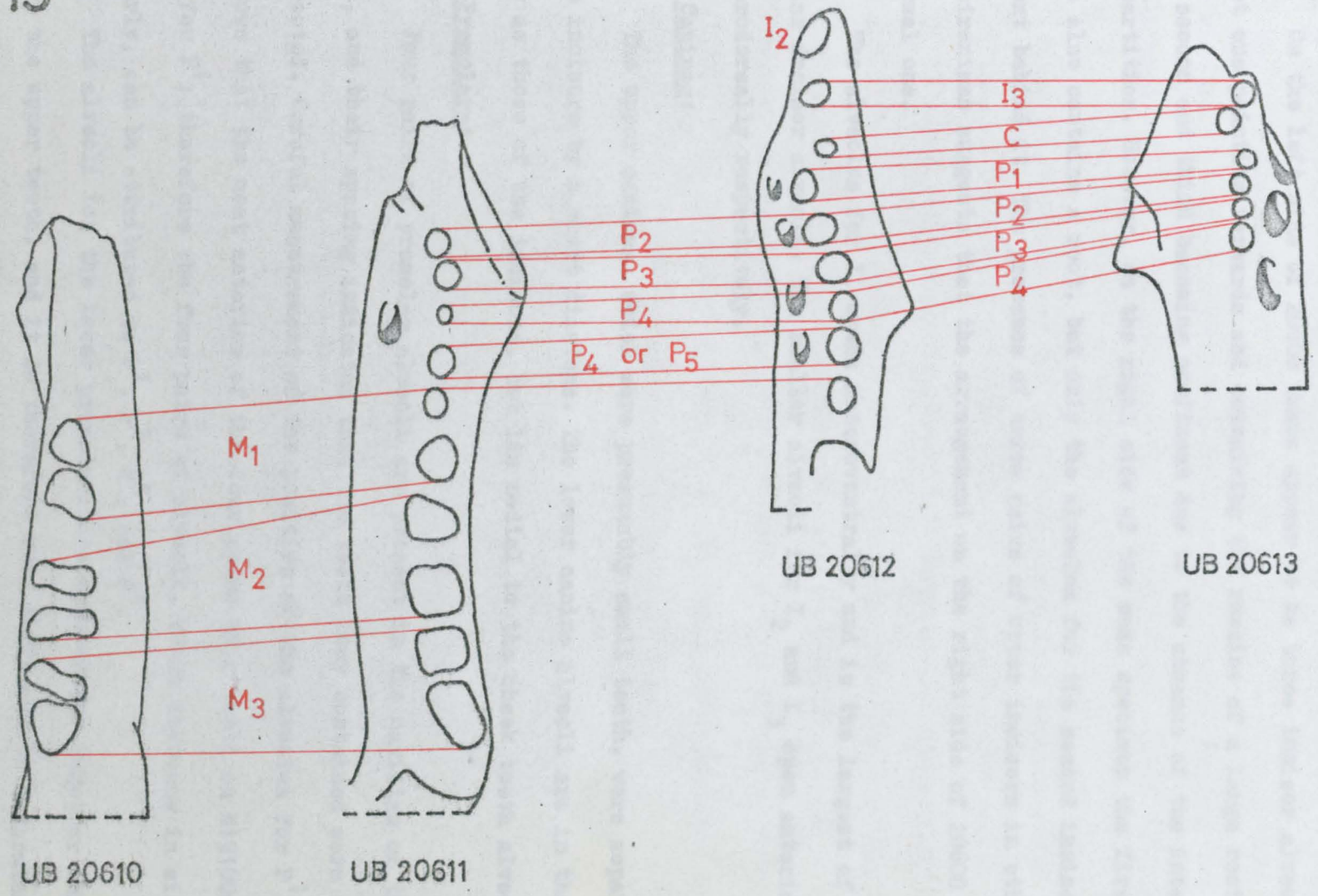
Dental Formula (Plate 13: Figure 19):

The upper dentition is only known from the alveoli - the premaxillary alveoli on 20608 and the maxillary alveoli on M19100a. The rostrum (20608) exhibits an asymmetrical arrangement of alveoli (see Plates 2 and 3), but on the left side at least there appears to have been a full complement of three incisors. The alveolus for the canine is present on both sides, although its size indicates a small tooth. The maxillary alveoli are very badly preserved and it is only by comparing both maxillae that it is possible to calculate the number of cheek teeth present. The remains of alveoli for six cheek teeth (P^1-M^2) are visible, but the posterior part of both maxillae is broken and all traces of M^3 have vanished.

The mandible is represented by fragments from six individuals and a composite picture of the complete lower dental sequence can be produced by carefully comparing the different pieces. Each half of the mandible contains a total of fifteen alveoli that are arranged in two distinct rows because the alveoli for the incisors and the canine are displaced mediad in relation to the alveoli for the cheek teeth (see Figure 19). Five out of the eleven cheek tooth alveoli can be attributed to the premolars, but it is difficult to estimate the actual number of premolars represented because it is not known if any of them were double-rooted. However, Sickenberg (1934) came to the conclusion that Protosiren had five single-rooted premolars in the mandible. The six alveoli referable to the molars represent the remains of three double-rooted teeth.

The tentative dental formula is thus:

FIG. 19 Comparison of edentulous mandibles of Libysiren sickenbergi gen. et sp. nov. x5/8



$$I\ \frac{3}{3},\ C\ \frac{1}{1},\ P\ \frac{4}{4\text{ or }5},\ M\ \frac{3}{3}$$

Teeth (Plates 12 and 13; Figure 20):

Incisors:

On the left side of 20608 there appear to be three incisor alveoli; the first one pointing forwards and containing the remains of a large root, and the second and third becoming confluent due to the absence of the intervening partition. However, on the right side of the same specimen the first alveolus also contains a root, but only the alveolus for the second incisor is present behind it. The presence of three pairs of upper incisors in other Eocene sirenians suggests that the arrangement on the right side of 20608 is an abnormal one.

The alveolus for I_1 opens anteroventrally and is the largest of the mandibular incisor alveoli. The smaller alveoli for I_2 and I_3 open anteriorly and anterodorsally respectively.

Canines:

The upper canines, which were presumably small teeth, were separated from the incisors by a short diastema. The lower canine alveoli are in the same row as those of the incisors, but lie medial to the cheek tooth alveoli.

Premolars:

Four pairs of premolar alveoli are present in the maxillae of the holotype, and their spacing indicates that the teeth they contained were all single-rooted. Careful measurement of the position of the alveolus for P^1 on 20608 shows that the most anterior of the four pairs of alveoli on M19100a is also for P^1; therefore the four pairs of alveoli, which increase in size posteriorly, can be attributed to P^1, P^2, P^3, and P^4.

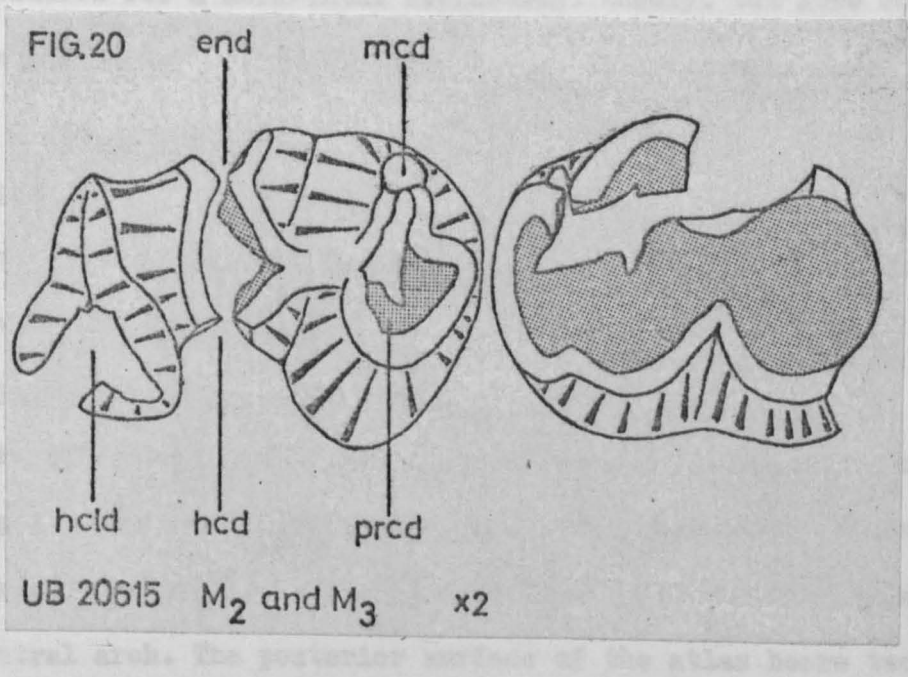
The alveoli for the lower premolars are much closer together than those for the upper teeth, and it is therefore more difficult to determine whether the lower premolars were single- or double-rooted. Evidence from other Eocene sirenians (e.g. Protosiren) supports the case for single-rooted teeth, but until more complete material is available it is impossible to say if the five premolar alveoli represent four or five actual teeth.

Molars (Plates 12 and 13; Figure 20):

Behind the upper premolar alveoli there are six larger alveoli that are distinctly arranged in two groups of three. These are the vestiges of M^1 and M^2, which, as in Eotheroides, each had two external roots and one internal one. Even the alveoli of M^3 are absent from M19100a because the maxillae are broken in this region, but there is enough space between the broken surfaces and the pterygoid processes to accommodate a third molar on each side.

Three lower molars are the only teeth known from remains other than the roots and/or alveoli, and they comprise two isolated and broken crowns (20615) and a tooth fragment attached to M19100b. The alveoli for the lower molars are much larger than those for the lower premolars and they are also anteroposteriorly compressed. Each molar had two roots.

The two isolated tooth crowns represent a right M_2 and M_3 from the same individual - the posterior surface of the M_2 has a facet produced by contact with the M_3, but the latter tooth has no such facet.



The M_2 is very worn and its occlusal surface is almost flat (see Figure 20). The heavy wear has obliterated the individual cusps, but the bilophid structure of the tooth is still visible. The protolophid (metaconid and protoconid) appears to have been larger than the metalophid (entoconid

and hypoconid), and the latter is followed by an extremely worn area that corresponds to the hypoconulid. The lingual side of the metalophid is higher than the labial side.

The wear on the M_3 has not been as extensive as on the M_2 and thus more of the tooth's structure is visible. It is longer than the preceding tooth because its hypoconulid is more prominent and gives the tooth a trilophid appearance. The protolophid and metalophid are joined by a narrow bridge of enamel and are most worn on their labial sides.

The tooth fragment attached to M19100b is undoubtedly a molar because of its position at the rear of the tooth row (see Plate 13). The little of it that remains, a single unworn cusp surrounded by a prominent cingulum, gives the erroneous impression that it was an almost circular tooth when complete. Neither of the teeth described above bears a cingulum, but this may be due to their stage of wear.

The difference in the amount of wear between M_2 and M_3 could be used as evidence for a horizontal replacement theory, but more complete material needs to be studied before this can be demonstrated.

Vertebrae:

Only two vertebrae are known - the atlas (M19100c) and an anterior thoracic vertebra (M19100d).

Cervical vertebrae (Figure 21):

The atlas vertebra is large and is very well preserved on the holotype. It possesses two large cotylar facets that are widest dorsally and become narrower ventrally, although they do not meet on the anterior surface of the ventral arch. The posterior surface of the atlas bears two sub-cordate facets that articulate with the axis; these also do not extend onto the ventral arch. The dorsal arch is wide and has a large superior tubercle for attachment of the rectus posticus muscle. The ventral arch is about half as wide as

FIGURE 21

Libycairen sickenbergi gen. et sp. nov.

M19100c

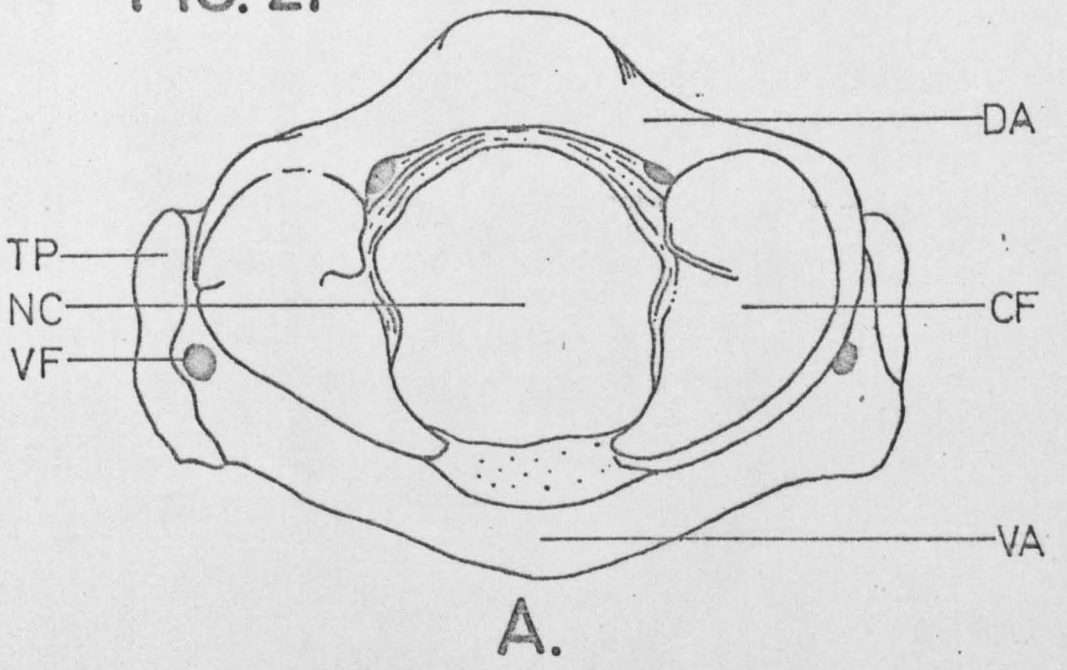
A: anterior view of atlas vertebra

B: dorsal view of atlas vertebra

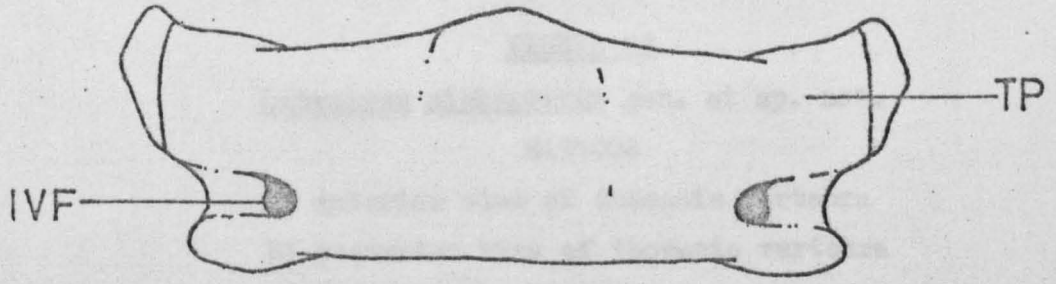
C: posterior view of atlas vertebra

$\frac{x2}{3}$

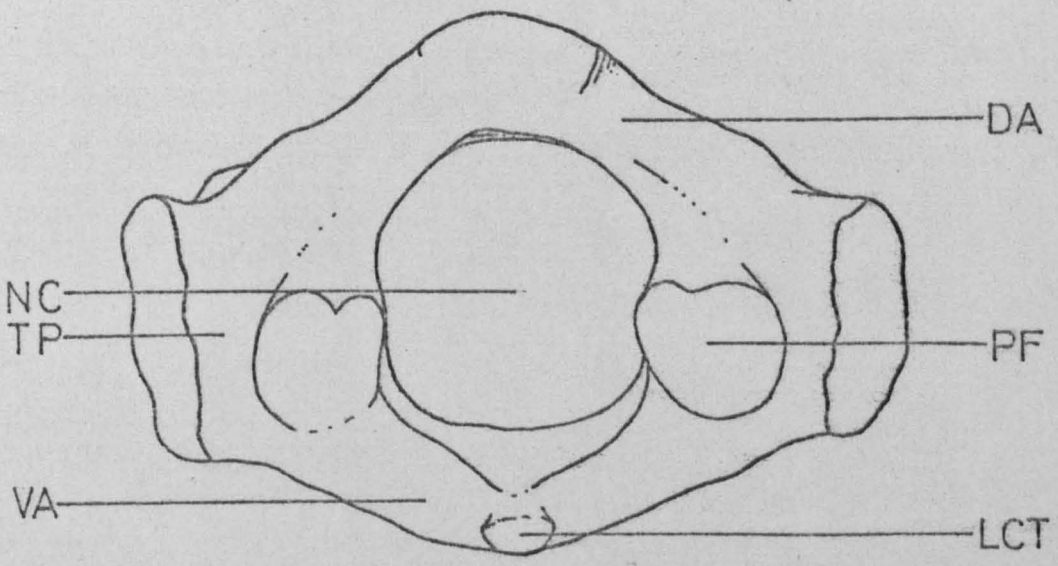
FIG. 21



A.



B.



C.

FIGURE 22

Libysiren sickenbergi gen. et sp. nov.

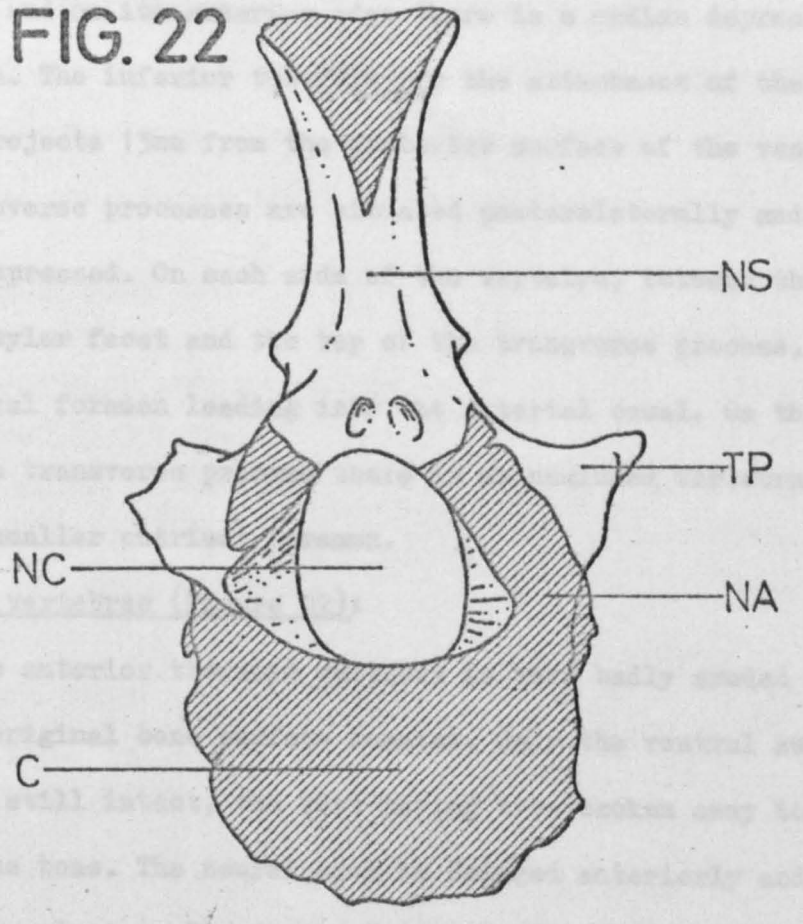
M19100d

A: anterior view of thoracic vertebra

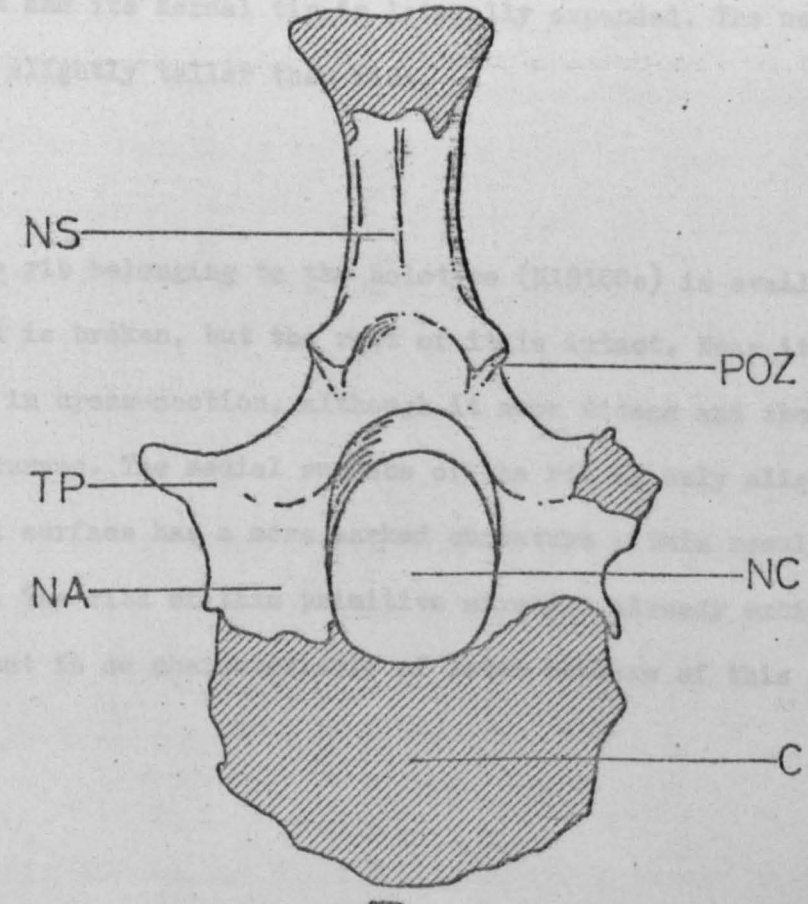
B: posterior view of thoracic vertebra

$x \frac{1}{0.5}$

FIG. 22



A.



B.

the dorsal one and on its anterior edge there is a median depressed area c.22mm in width. The inferior tubercle for the attachment of the longus colli muscle projects 13mm from the posterior surface of the ventral arch. The short transverse processes are situated posterolaterally and are antero-posteriorly compressed. On each side of the vertebra, between the dorsal edge of the cotylar facet and the top of the transverse process, there is an intervertebral foramen leading into the arterial canal. On the anterior surface of each transverse process there is an occluded vertebrarterial foramen and a smaller nutrient foramen.

Thoracic vertebrae (Figure 22):

The one anterior thoracic vertebra is very badly eroded and very little of the original bone surface remains. Only the ventral surface of the centrum is still intact, the rest having been broken away to expose the structure of the bone. The neural arch is damaged anteriorly and the pre-zygapophyses are missing. The postzygapophyses are present and intact, and they arise from the base of the neural spine. The bases of the transverse processes are present, but their lateral ends are broken. The vertical neural spine is robust and its dorsal tip is laterally expanded. The neural canal is oval, being slightly taller than wide.

Ribs:

A large rib belonging to the holotype (M19100e) is available for study. Its head is broken, but the rest of it is intact. Near its head the rib is angular in cross-section, although it soon widens and the angles give way to smooth curves. The medial surface of the rib is only slightly curved, but the lateral surface has a more marked curvature - this results in a D-shaped section. The ribs of this primitive sirenian already exhibit the pachyostosis that is so characteristic of later members of this order.

Comparison and discussion:

The most striking feature about the skull of Libysiren sickenbergi is that it is much larger than that of any other Eocene sirenian. The overall lengths of the skulls of seven Eocene species are as follows:

Prorastomus sirenoides Owen	267mm+	1
Protosiren fraasi Abel	300-365mm	2, 3
Libysiren sickenbergi gen. et sp. nov.	452mm+	1
Eotheroides aegyptiacum (Owen)	258mm	3
E. libycum (Andrews)	280-320mm	3
E. stromeri (Abel)	300mm	3
Prototherium veronense de Zigno	342mm	3

Sources

1 author's notes
2 Andrews (1906)
3 Sickenberg (1934)

The only species that approaches the size of Libysiren is Prototherium veronense, but even that species is still only three-quarters of the size of the Libyan genus.

Sickenberg (1934) has produced a list of anatomical features that can be used to differentiate between Eotheroides-Prototherium and Protosiren. I have used a modified version of this list in order to compare Libysiren with these other Eocene genera, and it can be seen from this table (see Table 5) that the new genus is closest to Protosiren.

The premaxillae of Libysiren are very similar in shape to those of both Eotheroides and Protosiren, but Sickenberg (ibid.) separated the latter two genera on the position of the premaxilla-maxilla suture. In Libysiren the relationship of these two bones is the same as in Protosiren - i.e. with the suture much further back than the premaxillary symphysis. The mesorostral fossa is bounded by a single arch and not a double arch as is the case in Protosiren (Sickenberg, ibid., fig. 6) and Eotheroides sp. (Reinhart, 1959, fig. 8).

The relationship between the maxilla and the jugal cannot be clearly

discerned because of the poor preservation of the bone in this region. Reinhart (ibid.) illustrated a very well preserved jugal of Eotheroides sp. that distinctly reaches the lacrimal, but the situation in Libysiren is not so well marked.

The arrangement of the nasals and frontals of sirenians has been used by Kretzoi (1941) and Kaltenmark (1943) to distinguish the different species, and Reinhart (1959) has amalgamated the views of these two authors to produce a theory of divergence during the Eocene amongst the species of Eotheroides. The nasals of Libysiren are like those of Protosiren in general outline, but but they are longer in relation to the dimensions of the frontals (see Figure 23). The nasals are not forcibly separated by the frontals as in Eotheroides aegyptiacum and E. libycum, but a small median extension of the frontals does overlap them posteriorly.

The lacrimal bone is unknown in Protosiren, although it has been described in detail for E. aegyptiacum (Abel, 1913) and E. sp. (Reinhart, 1959). Even though these two authors were dealing with the same genus, there are some noticeable differences between the lacrimal bones that they describe. The most noticeable difference is that Abel described the lacrimal as being completely surrounded by the maxilla, whereas Reinhart found that the jugal meets the ventral edge of the lacrimal. This variation is probably due to the better preservation of the antorbital region in Reinhart's specimen. Andrews' (1906) and Sickenberg's (1934) reconstructions of the skull of Protosiren fraasi show the premaxilla extending back between the lateral edge of the nasal and the medial edge of the supraorbital process of the frontal; neither of them shows the lacrimal and Sickenberg stated that this bone was not present on any of the specimens that he examined. The lacrimal of Libysiren occupies a position that is very different from that of any of the specimens of Eotheroides. Its relationships with the surrounding bones are described above, but its most distinctive feature is that it fills the space between the nasal and the supraorbital process so that the premaxilla is excluded from this area. The absence of a lacrimal foramen and duct is an

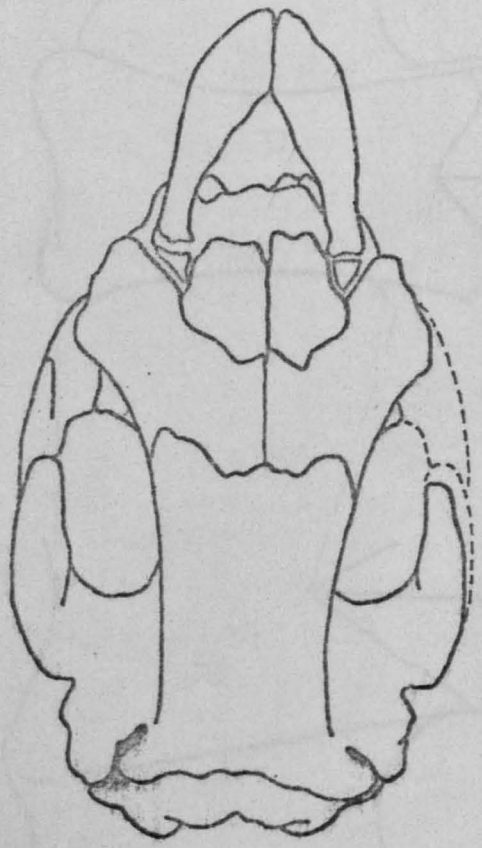
FIGURE 23

Dorsal views of the skulls of four genera of Eocene sirenians showing the variation in size and shape. All skulls x¼

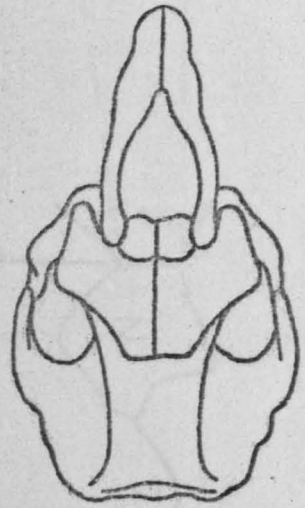
FIGURE 24

Skull roofs of two protosirenids (A) and two eotheroidids (B) showing the shorter nasals, longer frontals, and shorter parietals of the more advanced member of each family. All skulls reduced to the same nasal-frontal-parietal length.

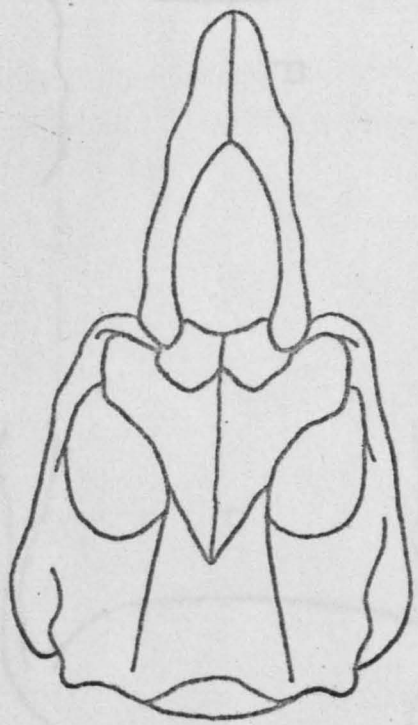
FIG. 23



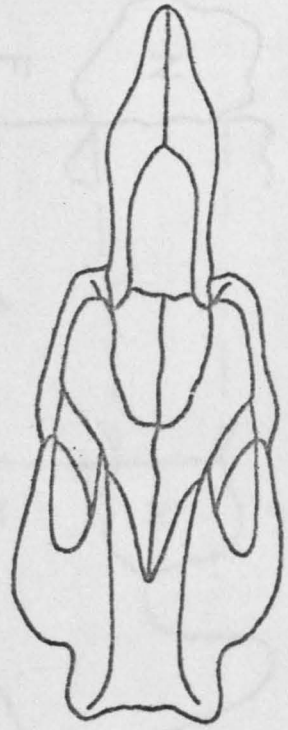
Libysiren
gen. nov.



Protosiren

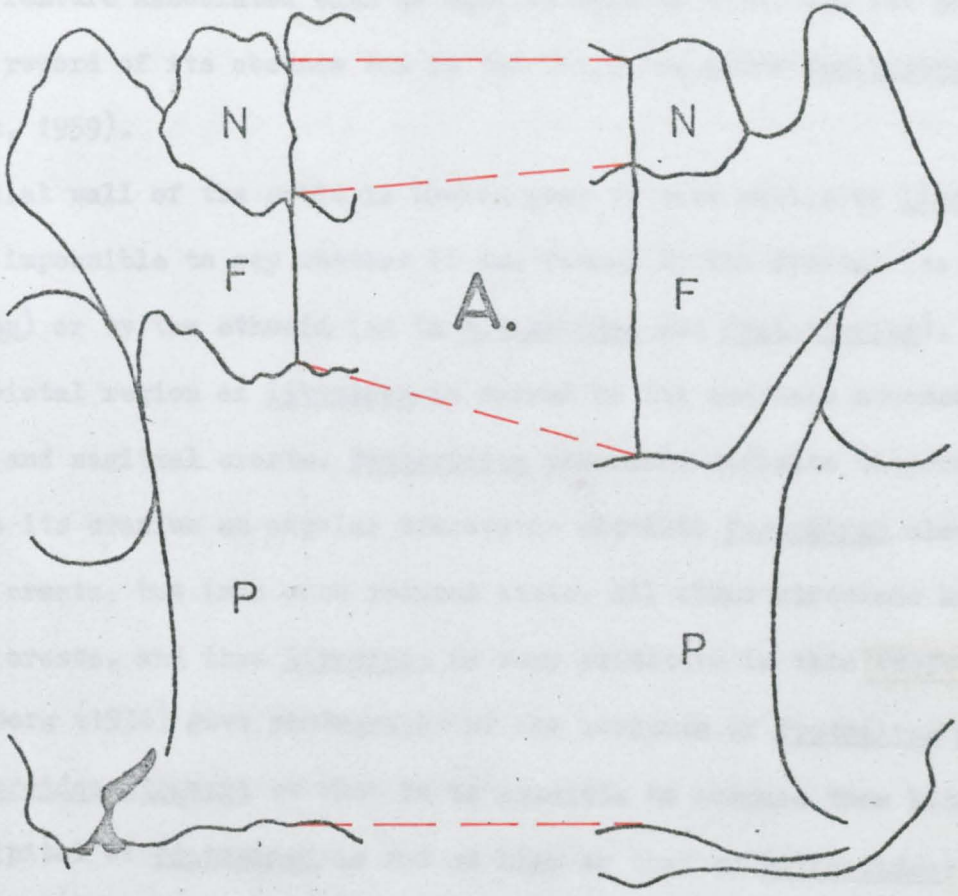


Eotheroides

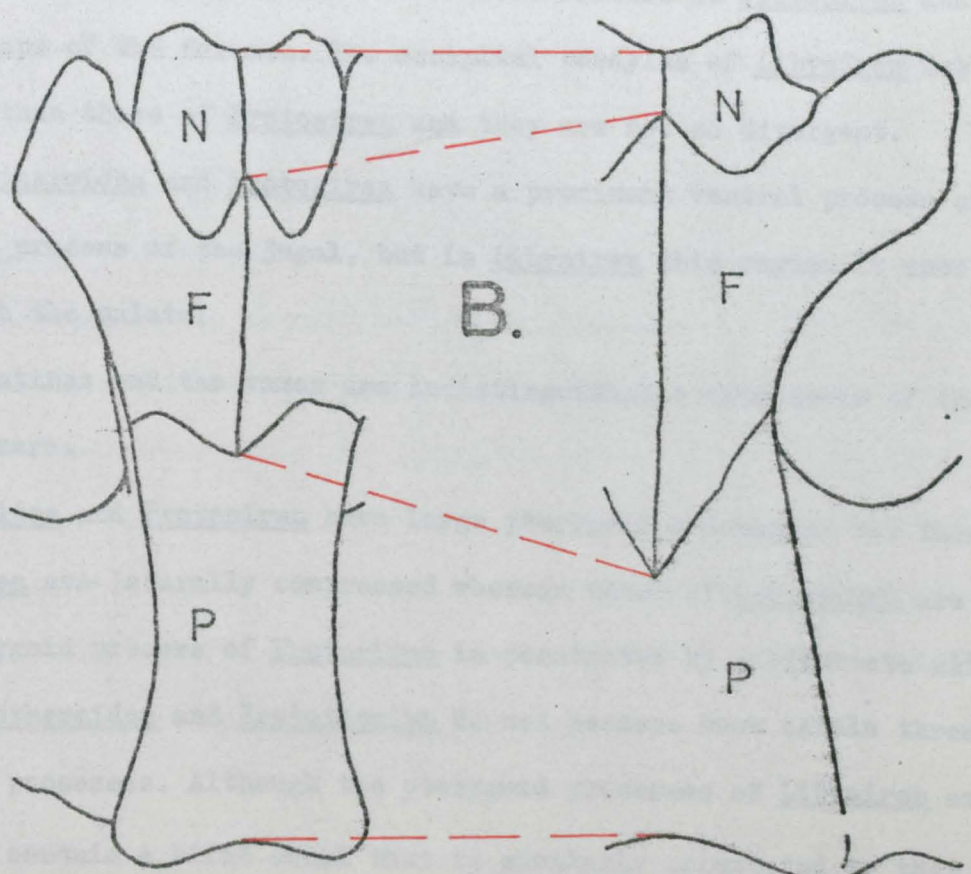


Prototherium

FIG. 24



Libysiren Protosiren



E. aegyptiacum E. stromeri

advanced feature associated with an aquatic mode of life, and the previous earliest record of its absence was in the Oligocene genus Caribosiren (Reinhart, 1959).

The medial wall of the orbit is broken away in both skulls of Libysiren; so it is impossible to say whether it was formed by the frontal (as in Protosiren) or by the ethmoid (as in Eotheroides and Prototherium).

The parietal region of Libysiren is marked by the complete absence of temporal and sagittal crests. Eotheroides possesses definite temporal crests that give its cranium an angular transverse section; Protosiren also has temporal crests, but in a much reduced state. All other sirenians have temporal crests, and thus Libysiren is very primitive in this respect.

Sickenberg (1934) gave photographs of the occiputs of Protosiren fraasi and Eotheroides stromeri so that it is possible to compare them both. The supraoccipital of Protosiren is not as high as that of Eotheroides; so the occiput appears broader in the former. The occiput of Libysiren more closely resembles that of Eotheroides in general outline. In Libysiren, the supra-occipital does not reach the dorsal margin of the foramen magnum, but according to Sickenberg this is a variable feature in Protosiren and depends on the shape of the foramen. The occipital condyles of Libysiren are broader dorsally than those of Protosiren and they are not so divergent.

Both Eotheroides and Protosiren have a prominent ventral process on the zygomatic process of the jugal, but in Libysiren this region is smooth and level with the palate.

The palatines and the vomer are indistinguishable from those of the other Eocene genera.

Eotheroides and Protosiren have large pterygoid processes, but those of Eotheroides are laterally compressed whereas those of Protosiren are broader. Each pterygoid process of Protosiren is penetrated by a bifurcate alisphenoid canal ; Eotheroides and Prototherium do not possess such canals through their pterygoid processes. Although the pterygoid processes of Libysiren are broken, they also contain a bifid canal that is similarly orientated to that of

Protosiren. The presence of an alisphenoid canal is thus a diagnostic character for the Protosirenidae (cf. presence of an alisphenoid canal in otariid and odobenid pinnipeds, but its absence in phocid pinnipeds). The other foramina of the orbito-sphenoid region (the optic foramen, the ethmoidal foramen, and the sinus canal foramen) occupy similar positions in Eotheroides, Protosiren, and Libysiren.

The squamosals of Libysiren exhibit a combination of Eotheroides and Protosiren features. In Eotheroides, the squamosaland the occipital meet and the squamosal forms part of the back of the skull; in Protosiren and Libysiren the parietal sends a narrow projection between these two bones and limits the squamosal to the side of the skull. The zygomatic process of the squamosal is deeper in Libysiren than in either of the other two genera, and it most closely resembles the zygomatic process of Trichechus. The superficies meatus is elongated as in Protosiren, but behind it there is a prominent post-tympanic process that is also found in Eotheroides but not in Protosiren.

The mesethmoid is similar to that of Protosiren.

The petrotympanic of Libysiren has a large processus fonticulus that fills the fonticulus mastoideus, and this is also the case in Protosiren. In other respects the ear region is similar to that of the other two genera.

Eotheroides and Protosiren have been distinguished by the differences in structure of their endocranial casts (Edinger, 1939), and the genus Eotherium (=Eotheroides) was in fact erected on the basis of such a cast (Owen, 1875). The differences amount to the presence or absence of an ossified falx cerebri and/or tentorium cerebelli — Eotheroides has both, but Protosiren has only an ossified tentorium cerebelli. Libysiren agrees with the condition found in Protosiren, but the significance that can be attached to such features is very dubious. In a group that shows marked pachyostosis, the presence or absence of such variable characters should not be relied upon for generic allocations as has been the case in the past.

The mandible of Libysiren is basically an enlarged version of that of

Eotheroides or Protosiren, but the shape of the ascending ramus is unlike that of Eotheroides or the later dugongids. Whereas the ascending ramus of Eotheroides rises vertically from the horizontal ramus, that of Libysiren is inclined forwards as on the mandible of Trichechus. The ascending ramus of Protosiren is unknown.

The difficulty of calculating the dental formula was mentioned above and this feature is therefore unusable as a diagnostic character. If the complete dental formula of Libysiren was known with certainty it would be possible to compare it with the known formulas of Eotheroides and Protosiren.

The badly worn M_2 of Libysiren resembles that of Protosiren, but the M_3 differs from the corresponding tooth in both Protosiren (Sickenberg, 1934) and Eotheroides (Abel, 1913). The difference occurs in the size and shape of the hypoconulid, which is longest in the mid-line in Eotheroides but longest labially in Libysiren. The hypoconulid on the M_3 of Protosiren is very small, but Abel (ibid.) illustrated two M_3's from E. aegyptiacum that show that there is a great variation in the size of this part of the tooth.

The atlas vertebra of Libysiren more closely resembles that of Eotheroides than it does that of Protosiren. The superior tubercle on the dorsal arch is low and broad as in Eotheroides, and the cotylar facets extend onto the ventral arch unlike in Protosiren where they are restricted to the sides of the vertebra.

The anterior thoracic vertebra does not differ markedly from those of Eotheroides or Protosiren.

The following table of comparisons has been adapted from Sickenberg (1934, pp. 192-193):

TABLE 5

Eotheroides-Prototherium	Libysiren	Protosiren
1. Premaxilla-maxilla suture below symphysis.	As in Protosiren.	Premaxilla-maxilla suture much further back than symphysis.
2. Lacrimal surrounded by maxilla, frontal, and jugal.	Lacrimal surrounded by premaxilla, maxilla, nasal, and frontal.	?
3. Lacrimal duct present.	Lacrimal duct absent	?
4. Pronounced temporal crests.	No temporal crests.	Slight temporal crests.
5. Sagittal lengths of frontals and parietals in ratio of 1:1.3 (E. aegyptiacum)	Sagittal lengths of frontals and parietals in ratio of 1:2.4	Sagittal lengths of frontals and parietals in ratio of 1:1.3
6. Squamosal forms part of occiput.	As in Protosiren.	Squamosal does not form part of occiput.
7. Squamosal and supra-occipital meet.	As in Protosiren.	Squamosal and supraoccipital completely separated by a projection of the parietal.
8. Post-tympanic process of squamosal is present.	As in Eotheroides-Prototherium.	Post-tympanic process of squamosal is absent.
9. Superficies meatus is short.	As in Protosiren.	Superficies meatus is elongated.
10. Pterygoid processes are thin and lamellar.	As in Protosiren.	Pterygoid processes are thick and robust.
11. Alisphenoid canal absent.	As in Protosiren.	Alisphenoid canal present.
12. Periotic without processus fonticulus.	As in Protosiren.	Periotic with processus fonticulus.
13. Facial canal present.	As in Eotheroides-Prototherium.	Facial canal absent.
14. Ascending ramus of mandible is vertical.	Ascending ramus of mandible is inclined forwards.	?

The combination of both Eotheroides-Prototherium and Protosiren characters in Libysiren suggests that the Libyan genus may be ancestral to one or both of the former two groups. The fact that Libysiren occurs in the lower part of the Middle Eocene, whereas Eotheroides, Prototherium, and Protosiren are found

TABLE 5

Eotheroides-Prototherium	Libysiren	Protosiren
1. Premaxilla-maxilla suture below symphysis.	As in Protosiren.	Premaxilla-maxilla suture much further back than symphysis.
2. Lacrimal surrounded by maxilla, frontal, and jugal.	Lacrimal surrounded by premaxilla, maxilla, nasal, and frontal.	?
3. Lacrimal duct present.	Lacrimal duct absent	?
4. Pronounced temporal crests.	No temporal crests.	Slight temporal crests.
5. Sagittal lengths of frontals and parietals in ratio of 1:1.3 (E. aegyptiacum)	Sagittal lengths of frontals and parietals in ratio of 1:2.4	Sagittal lengths of frontals and parietals in ratio of 1:1.3
6. Squamosal forms part of occiput.	As in Protosiren.	Squamosal does not form part of occiput.
7. Squamosal and supra-occipital meet.	As in Protosiren.	Squamosal and supraoccipital completely separated by a projection of the parietal.
8. Post-tympanic process of squamosal is present.	As in Eotheroides-Prototherium.	Post-tympanic process of squamosal is absent.
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10. Pterygoid processes are thin and lamellar.	As in Protosiren.	Pterygoid processes are thick and robust.
11. Alisphenoid canal absent.	As in Protosiren.	Alisphenoid canal present.
12. Periotic without processus fonticulus.	As in Protosiren.	Periotic with processus fonticulus.
13. Facial canal present.	As in Eotheroides-Prototherium.	Facial canal absent.
14. Ascending ramus of mandible is vertical.	Ascending ramus of mandible is inclined forwards.	?

The combination of both Eotheroides-Prototherium and Protosiren characters in Libysiren suggests that the Libyan genus may be ancestral to one or both of the former two groups. The fact that Libysiren occurs in the lower part of the Middle Eocene, whereas Eotheroides, Prototherium, and Protosiren are found

in the upper part of the Middle Eocene and in the Upper Eocene, supports this suggestion. The predominance of protosirenid characters (especially 9, 10, and 11) favours a closer alliance to Protosiren than to Eotheroides or Prototherium. The Eotheroides-Prototherium characters and the few purely Libysiren characters (omitting 2, 3, and 14) can be taken to be very primitive features; in fact the absence of temporal crests and the fronto-parietal ratio are also characteristic of the most anatomically primitive, though not precisely dated, sirenian, Prorastomus sirenoides. In all post-Middle Eocene sirenians, temporal crests are present and the frontals and parietals are similar in sagittal length.

Superfamily DUGONGOIDEA superfam. nov.

Diagnosis: Rostrum enlarged and deflected. Numerically reduced dentition; incisor tusks usually present; premolars disappear in advanced genera. Broad bicipital groove on humerus; carpals tend to become fused; hind limbs reduced and functionless; ilium becomes rod-like. Seven cervical vertebrae; usually nineteen to twenty thoracic vertebrae.

Remarks: This superfamily contains only one family, the Dugongidae.

Family DUGONGIDAE Gray 1821

Diagnosis: As for superfamily.

Remarks: Six subfamilies can be recognized in the Dugongidae, the Halitheriinae, the Miosireninae, the Rytiodinae, the Metaxytheriinae, the Hydrodamalinae, and the Dugonginae.

Subfamily RYTIODINAE Abel 1928

Diagnosis: Rostrum strongly deflected; large lacrimal bone, but no lacrimal duct; narrow parietals. Large, flattened incisor tusks; cheek teeth enameled;

M^3 unreduced and complex.

Genus RYTIODUS Lartet 1866

Diagnosis: As for subfamily.

Type species: Rytiodus capgrandi Lartet 1866; Lower Miocene (Aquitanian) of Lot-et-Garonne and Gironde, France.

Distribution: Lower Miocene of France (Aquitanian) and Libya (Burdigalian).

Rytiodus zeltenensis sp. nov.

Diagnosis: Premaxillary rami abut against nasals; triangular lacrimal.

Etymology of specific name: Derived from the type locality - Gebel Zelten, Libya.

Holotype: BM(NH) M19101a-c. Skull, endocranial cast, and associated vertebrae and ribs. Site 64.19.

Paratypes:

	Site	
UB 20853a-e	64.19	skull, endocranial cast, and associated vertebrae and ribs
UB 20854	?	maxillary fragment
UB 20855a-b	?	two right tympanics
UB 20856	64.18	left mandibular ramus with M_3
UB 20857	64.20	three posterior thoracic vertebrae

Age and locality: Lower Miocene (Burdigalian) of Gebel Zelten (28°-29° N., 19° 30'-20° 30' E.), Libya.

Remarks: A provisional list of the vertebrate fauna from the Miocene of Gebel Zelten has been given by Savage & Hamilton (1973).

Anatomical description:

Skull (Plates 14, 15, 16, 18, and 19):

Most of the anatomical details of the skull were obtained from two individuals, both of which (M19101a and 20853a) have unfortunately suffered conspicuous damage. However, the features absent from one of the skulls tend to be intact on the other. 20853a is the most complete anteriorly and has

PLATE 14

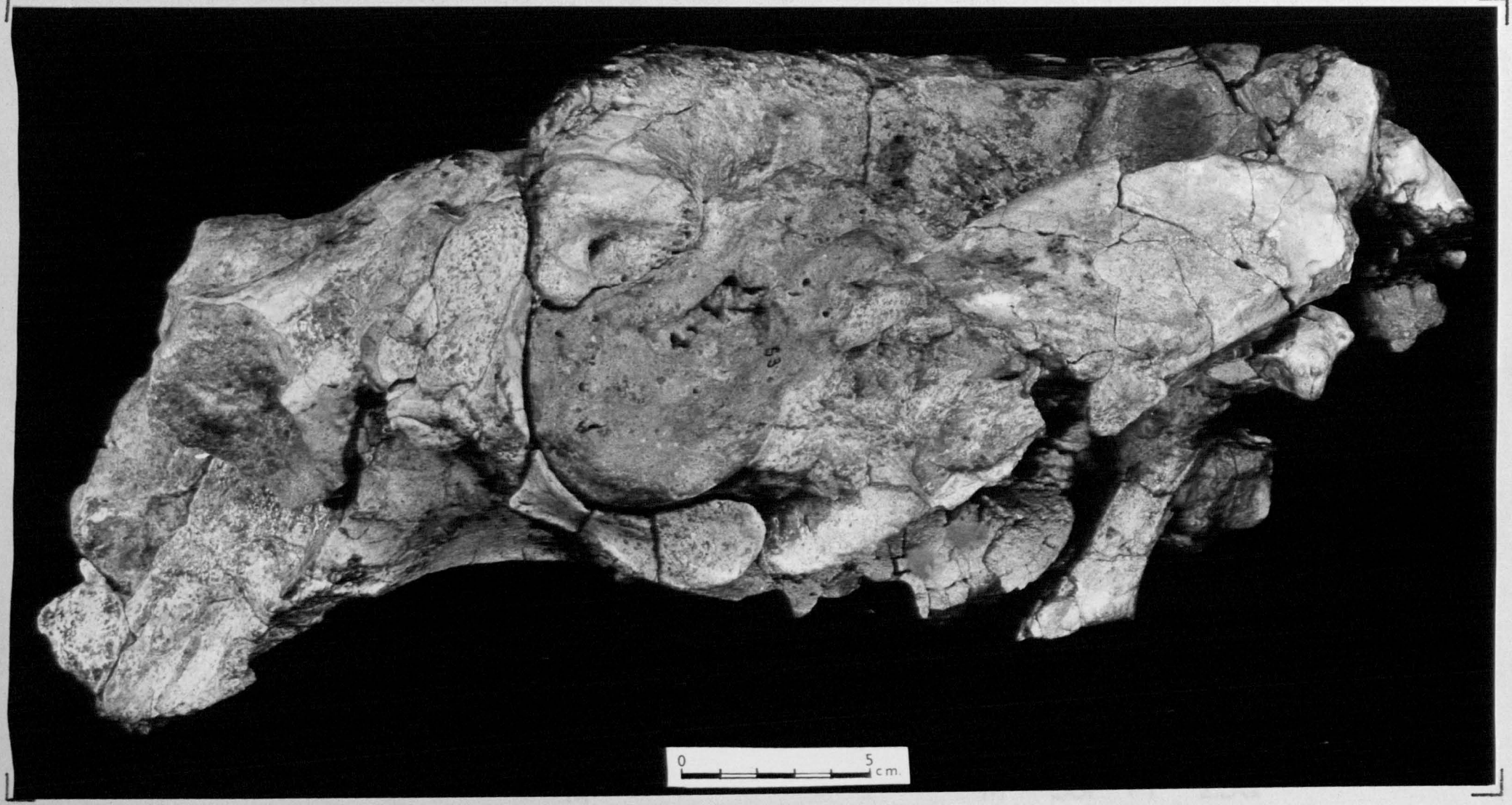
Rytiodus zeltenensis **sp. nov.**

M19101a : left lateral view of skull

FIGURE 25

Drawing of Plate 14

PLATE 14



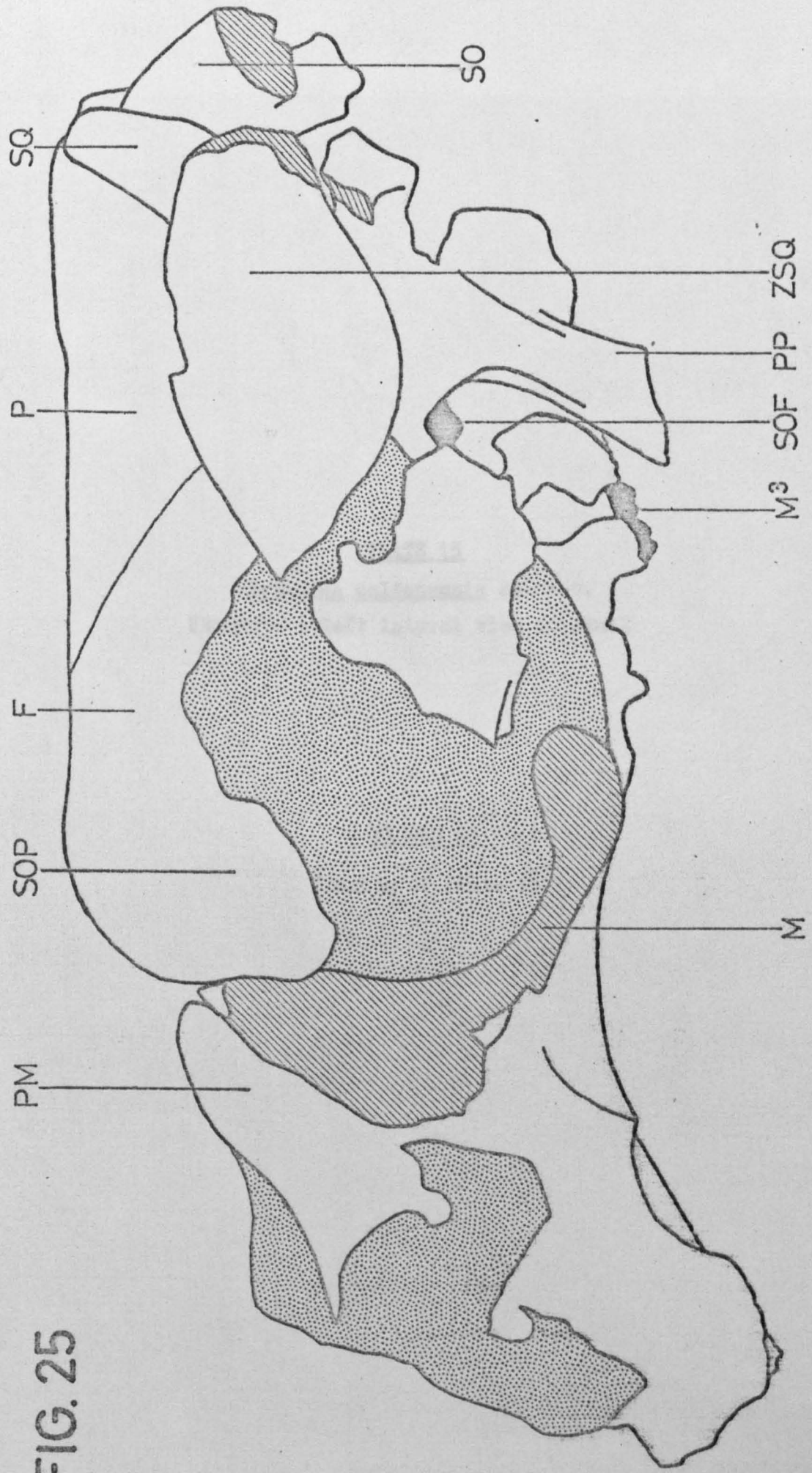


FIG. 25

PLATE 15

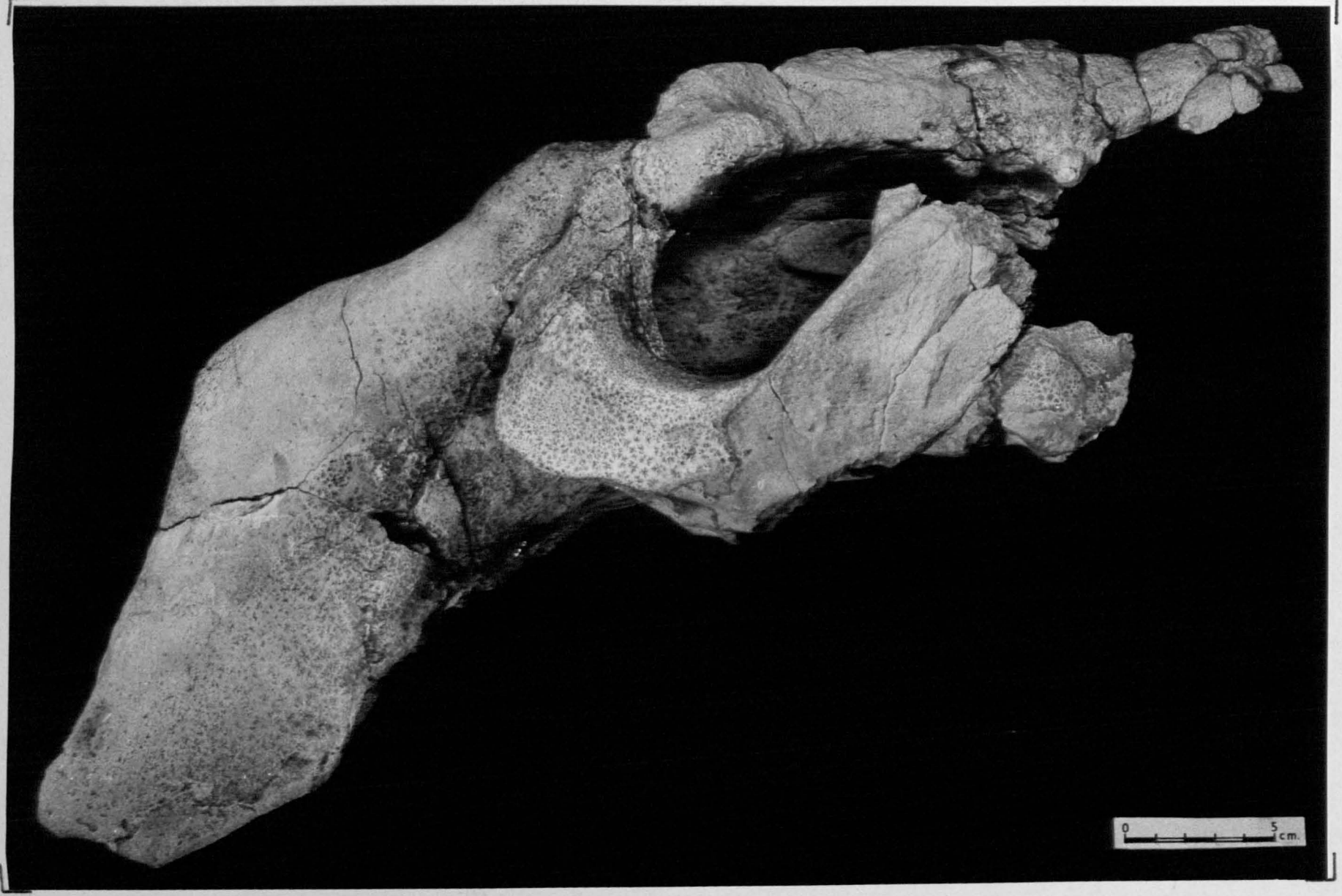
Rytiodus zeltenensis sp. nov.

UB20853a : left lateral view of skull

FIGURE 26

Drawing of Plate 15

PLATE 15



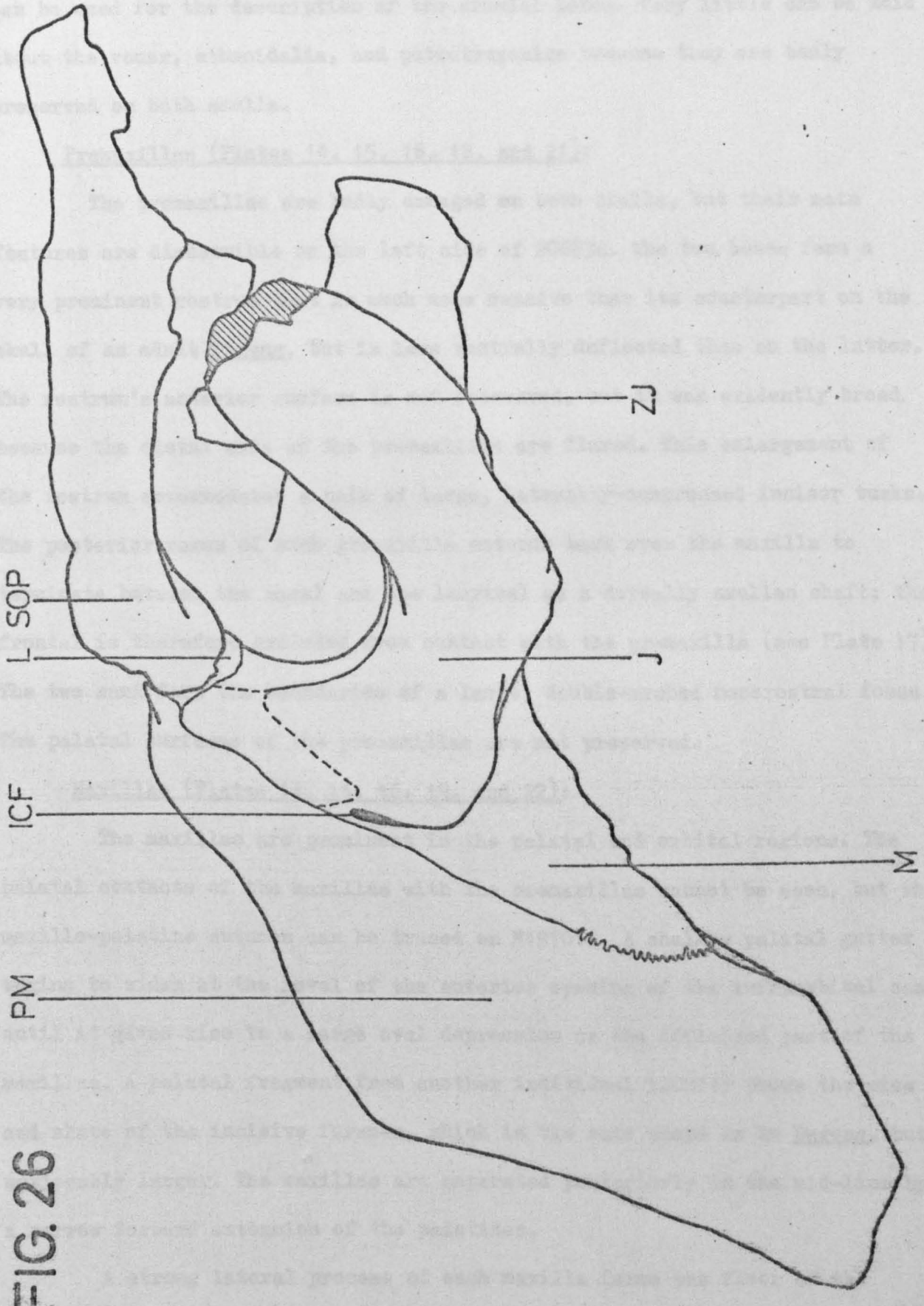


FIG. 26

been used for the description of the facial bones; M19101a is not so well preserved in the facial region, but is more complete around the braincase and can be used for the description of the cranial bones. Very little can be said about the vomer, ethmoidalia, and petrotympanics because they are badly preserved on both skulls.

Premaxillae (Plates 14, 15, 16, 18, and 21):

The premaxillae are badly damaged on both skulls, but their main features are discernible on the left side of 20853a. The two bones form a very prominent rostrum that is much more massive than its counterpart on the skull of an adult Dugong, but is less ventrally deflected than on the latter. The rostrum's anterior surface is not preserved, but it was evidently broad because the distal ends of the premaxillae are flared. This enlargement of the rostrum accommodates a pair of large, laterally-compressed incisor tusks. The posterior ramus of each premaxilla extends back over the maxilla to terminate between the nasal and the lacrimal as a dorsally swollen shaft; the frontal is therefore excluded from contact with the premaxilla (see Plate 17). The two rami form the boundaries of a large, double-arched mesorostral fossa. The palatal surfaces of the premaxillae are not preserved.

Maxillae (Plates 14, 15, 16, 19, and 22):

The maxillae are prominent in the palatal and orbital regions. The palatal contacts of the maxillae with the premaxillae cannot be seen, but the maxillo-palatine sutures can be traced on M19101a. A shallow palatal gutter begins to widen at the level of the anterior opening of the infraorbital canal until it gives rise to a large oval depression on the deflected part of the maxillae. A palatal fragment from another individual (20854) shows the size and shape of the incisive foramen, which is the same shape as in Dugong, but noticeably larger. The maxillae are separated posteriorly in the mid-line by a narrow forward extension of the palatines.

A strong lateral process of each maxilla forms the floor of the orbital cavity, then expands anteroposteriorly to produce an extensive surface for the attachment of the medial wall of the jugal. A small extension of the

PLATE 16

Rytiodus zeltenensis **sp. nov.**

UB20853a : ventral view of skull

FIGURE 27

Drawing of Plate 16


0
5
cm.

FIG. 27

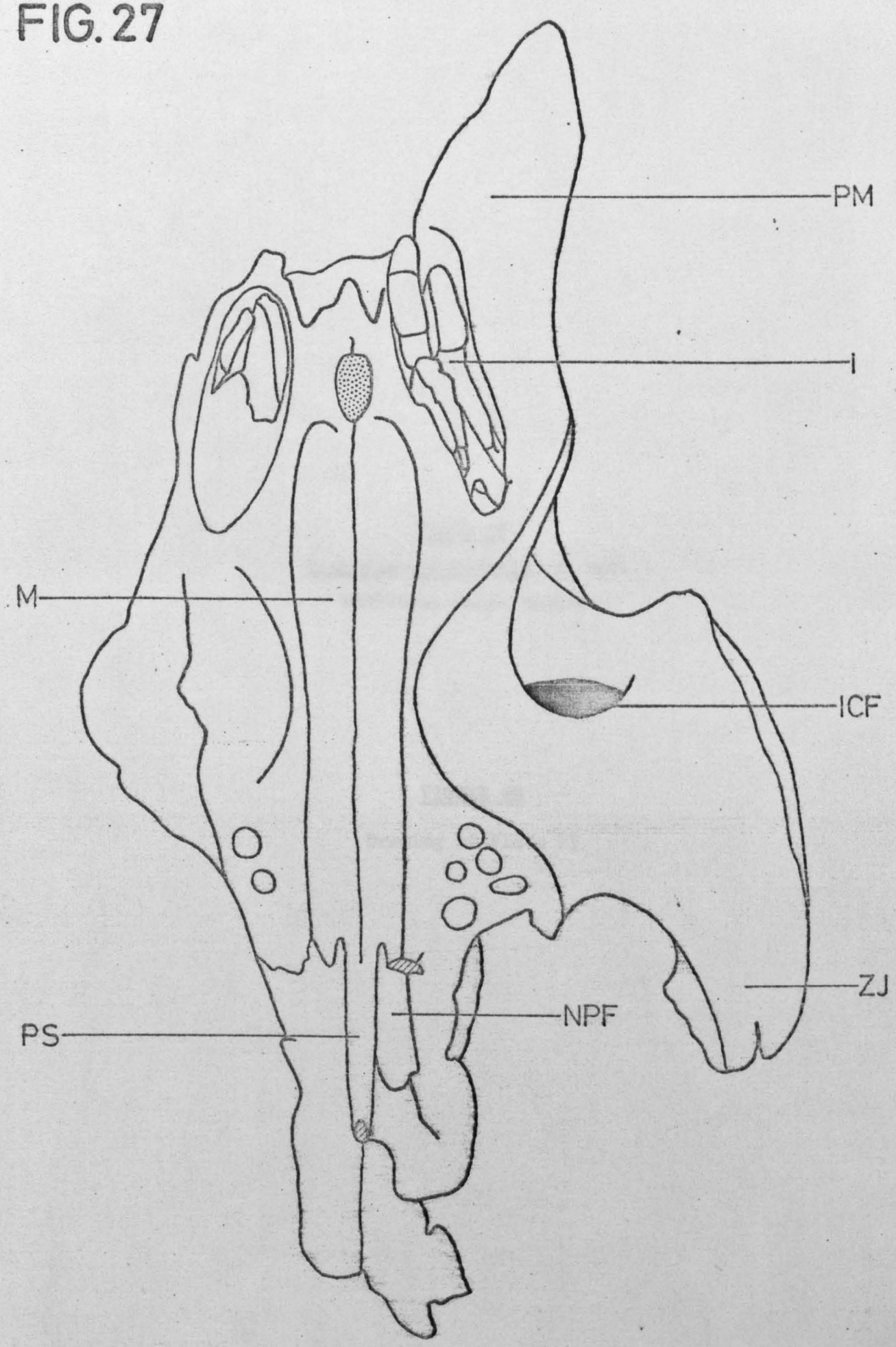


PLATE 17

Rytiodus zeltenensis sp. nov.

UB20853a: nasal region

FIGURE 28

Drawing of Plate 17

PLATE 17

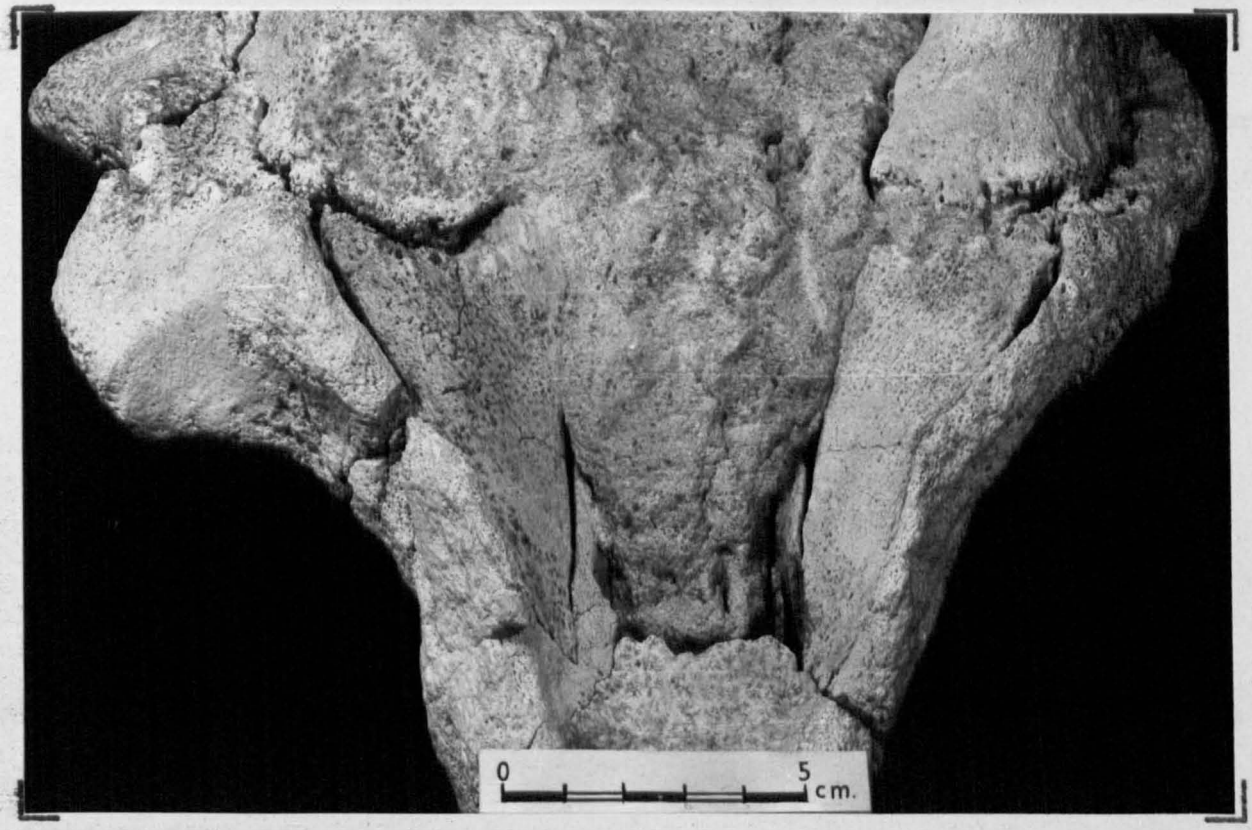
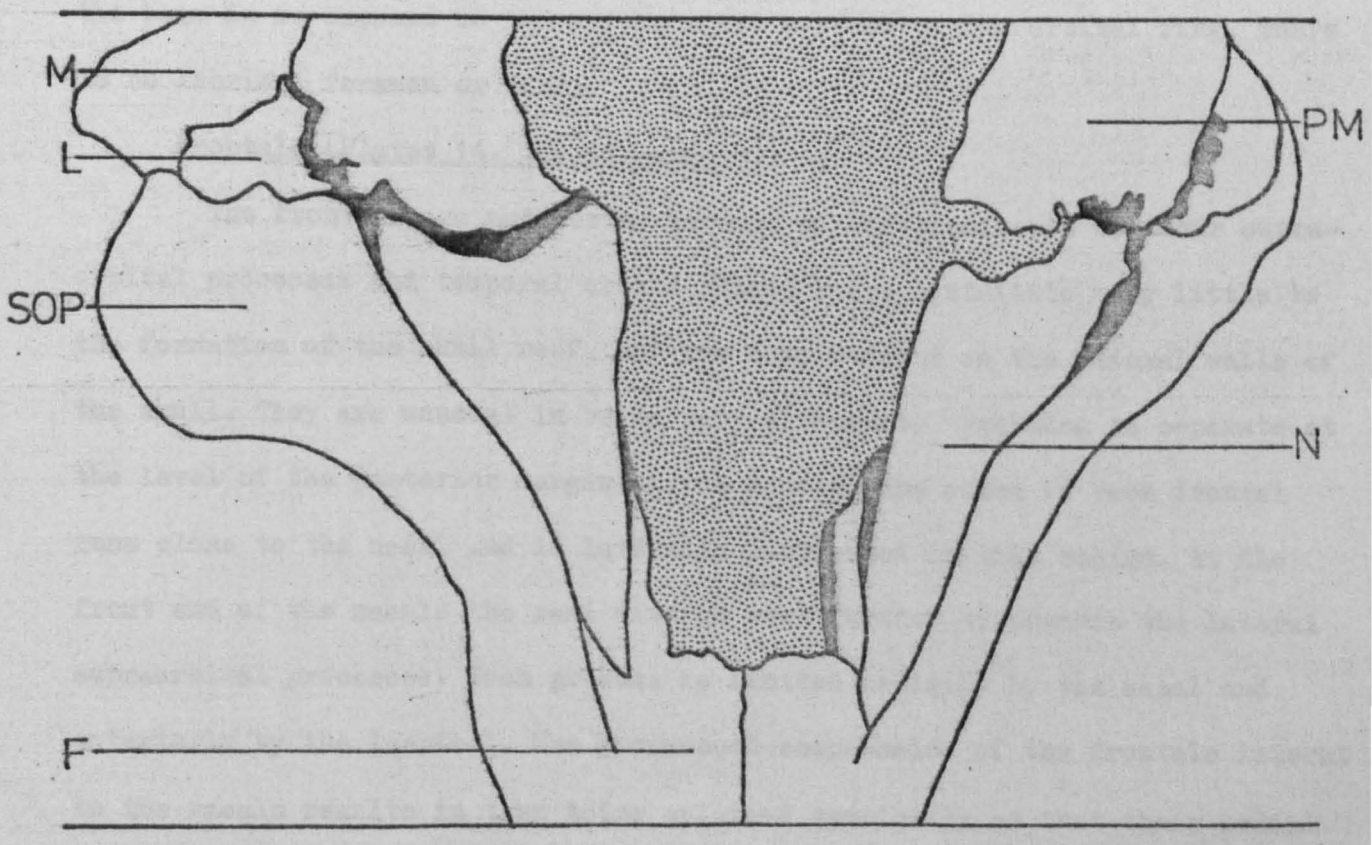


FIG. 28



maxilla appears to overlap the dorsal surface of the jugal component of the infraorbital foramen, but the relationships of the bones in this area are open to doubt. The orbital part of the maxilla is penetrated anteroposteriorly by a very wide infraorbital foramen, medial to which there is a prominent palatine foramen. An ill-defined ridge extends from the internal border of the palatine foramen to as far back as the external edge of the internal nares. The maxillae possess strong anterior processes that support the enlarged premaxillae.

Nasals (Plates 17 and 18):

The nasals are large triangular bones with their apices directed posteriorly. They are separated in the mid-line by the frontals, and the internal edge of each bone is directed ventromediad towards the mesorostral fossa. The nasals are bounded by the premaxillae anteriorly and by the frontals laterally and posteriorly.

Lacrimal (Plates 15, 17, and 18):

The lacrimal is well preserved on the left side of 20853a. It has its greatest exposure on the dorsal surface of the skull as a triangular bone. Its posterolateral corner extends ventrad between the maxilla and frontal, and the bone is re-exposed on the anterodorsal surface of the orbital ring. There is no lacrimal foramen or duct.

Frontals (Plates 14, 15, 17, and 18):

The frontals are noteworthy because of the prominence of their supraorbital processes and temporal crests. These bones contribute very little to the formation of the skull roof, but are more evident on the lateral walls of the skull. They are unusual in being very divergent, beginning to separate at the level of the posterior margin of the nasals. The ramus of each frontal runs close to the nasal and is laterally compressed in this region. At the front end of the nasals the rami diverge even further to produce the lateral supraorbital processes. Each process is limited medially by the nasal and anteriorly by the lacrimal. The pronounced compression of the frontals lateral to the nasals results in them being enlarged vertically so that their medial

PLATE 18

Rytiodus zeltenensis sp. nov.

M19101a: dorsal view of skull

FIGURE 29

Drawing of Plate 18

PLATE 18

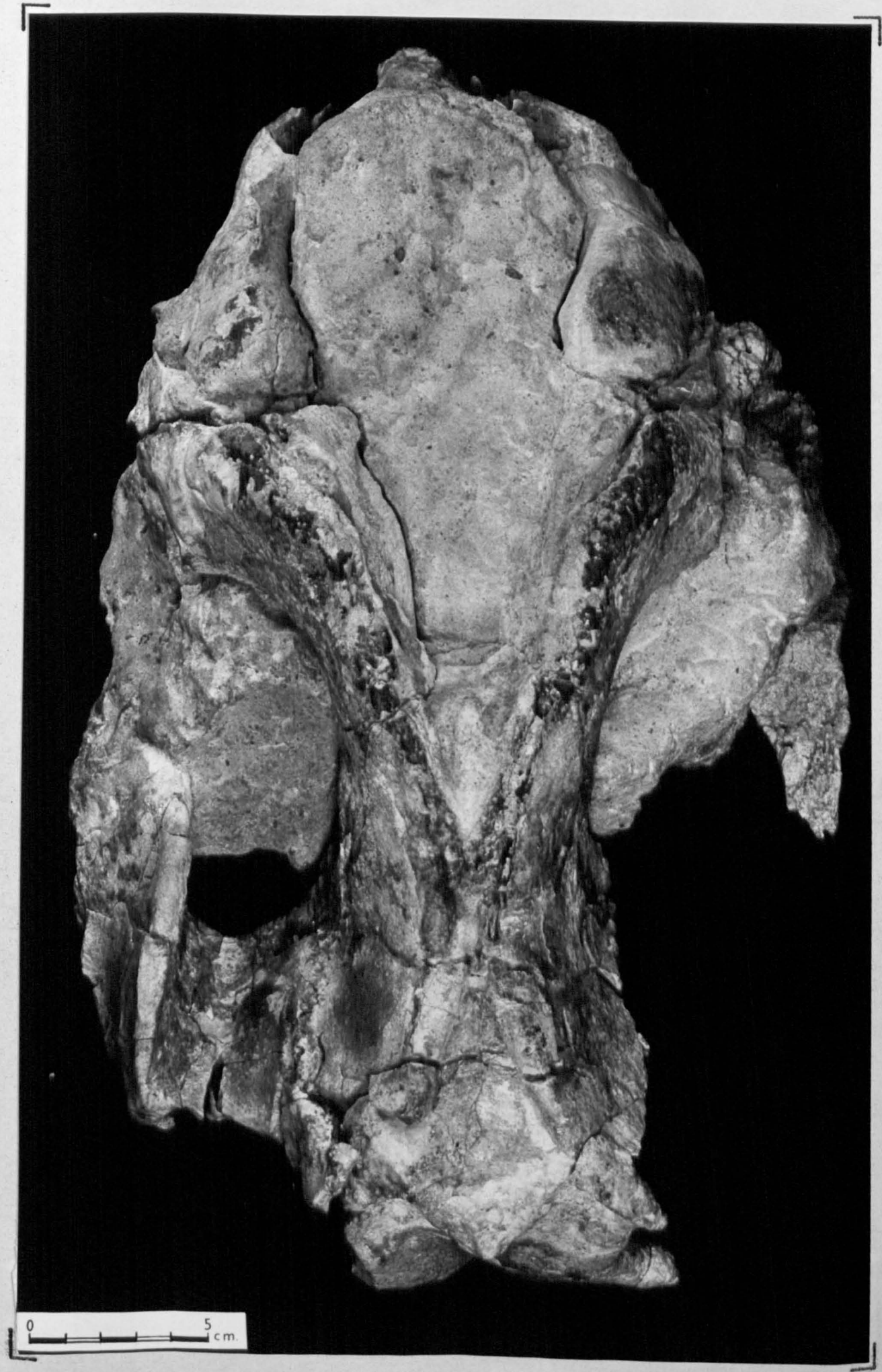
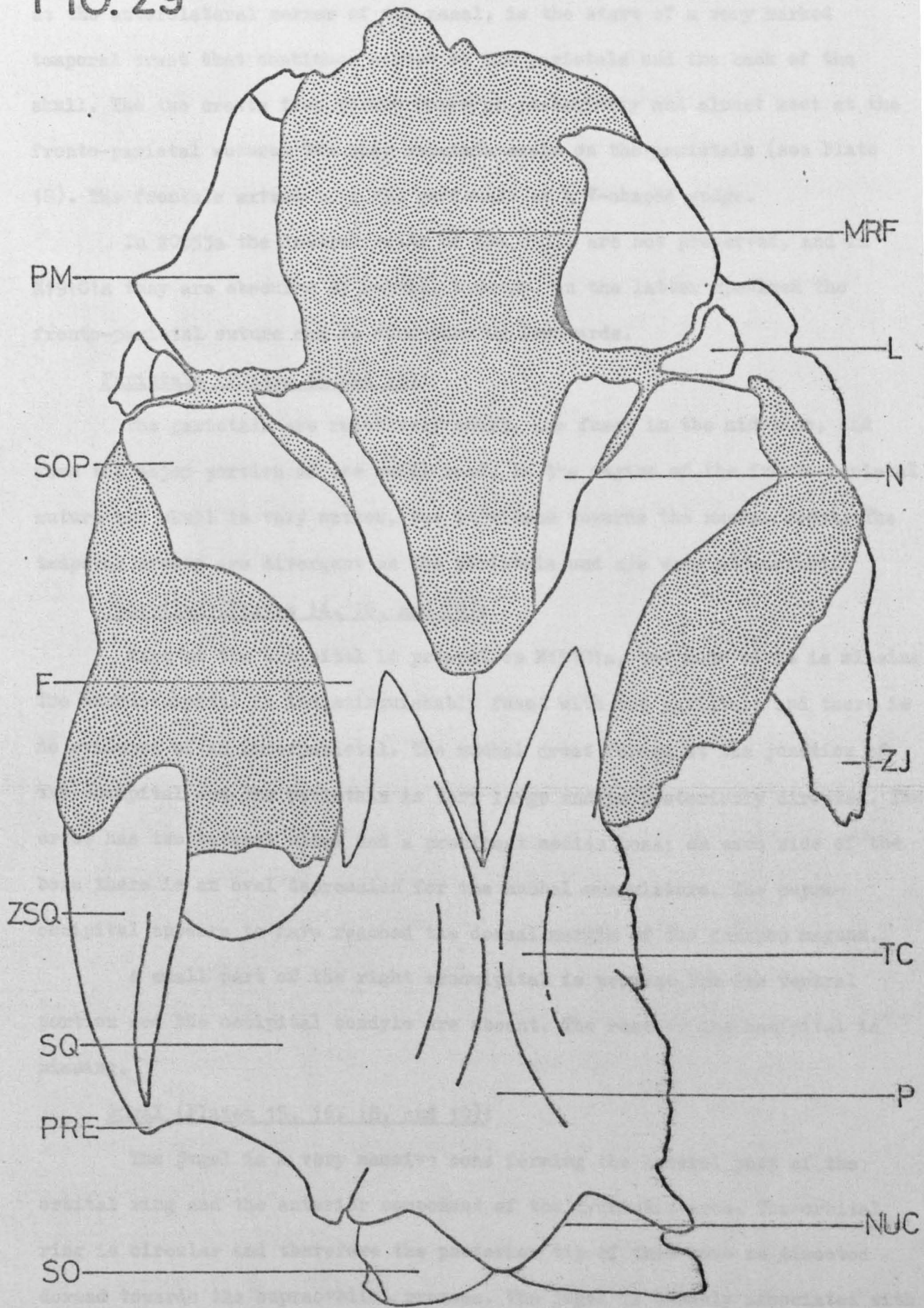


FIG. 29



edges are raised above the surface of the nasals. Each raised edge, beginning at the anterolateral corner of the nasal, is the start of a very marked temporal crest that continues across to the parietals and the back of the skull. The two crests thus formed converge posteriorly and almost meet at the fronto-parietal suture, but they separate again on the parietals (see Plate 18). The frontals extend into the parietals as a V-shaped wedge.

In 20853a the lateral walls of the skull are not preserved, and in M19101a they are obscured by matrix. However, on the latter specimen the fronto-parietal suture can be seen curving downwards.

Parietals (Plates 14 and 18):

The parietals are relatively short, are fused in the mid-line, and form the major portion of the skull roof. In the region of the fronto-parietal suture the skull is very narrow, but it widens towards the nuchal crest. The temporal crests are divergent on the parietals and are very pronounced.

Occipital (Plates 14, 18, and 19):

Part of the occipital is present on M19101a, but much of it is missing. The supraoccipital is indistinguishably fused with the parietals and there is no evidence of an interparietal. The nuchal crest formed at the junction of the occipital and the parietals is very large and is posteriorly directed. The crest has two lateral wings and a prominent median boss; on each side of the boss there is an oval depression for the nuchal musculature. The supra-occipital appears to have reached the dorsal margin of the foramen magnum.

A small part of the right exoccipital is present, but its ventral portion and the occipital condyle are absent. The rest of the occipital is missing.

Jugal (Plates 15, 16, 18, and 19):

The jugal is a very massive bone forming the lateral part of the orbital ring and the anterior component of the zygomatic arch. The orbital ring is circular and therefore the posterior tip of this bone is directed dorsad towards the supraorbital process. The jugal is closely associated with the maxilla, and the area of its attachment occupies the whole external surface of the maxilla's lateral process. The jugal is barred from contact

with the bones of the skull roof by a process of the maxilla that overrides its dorsal surface.

Palatines (Plates 19 and 22):

The relationships of the palatines with the surrounding bones are much the same as in Dugong. On the palate they form a narrow extension between the maxillae, but behind this they surround (and form the vertical walls of) a long, narrow, nasopharyngeal fossa that reaches as far forwards as M^1. The palatines continue back towards the vertical pterygoid laminae and end as thin, vertical laminae on the anteromedial surfaces of the latter.

Vomer:

The vomer is not visible on either skull.

Sphenoid (Plates 14, 16, 19, and 22):

The sphenoid complex is very fragmentary and its main features are obscured by extensive fracturing; therefore it is impossible to elucidate its structure as thoroughly as in Libysiren.

The rod-like presphenoid has discontinuous contacts with the orbitosphenoids and basisphenoid, and the orbitosphenoids are small and broken. The basisphenoid is a very robust bone that narrows towards its junction with the presphenoid; its exterior surface is convex, but internally it is flatter. The alisphenoids are more prominent than the rest of the complex, and the lateral arm of each forms part of the glenoid area although the sutures are not visible. The sphenorbital canal has been enlarged by the disintegration of its thin walls, but its position above the pterygoid process is well indicated. No other foramina are visible in the sphenoid region due to the very resistant matrix still adhering to the skull. The most prominent feature of each sphenoid is its stout, anteroventrally-directed pterygoid lamina, which combines with the palatine lamina to form the pterygoid process. In horizontal cross-section the ptergoid process is almost rectangular, but its posterior surface is grooved from base to tip (though not so markedly as in Dugong). The distal end of the process is flat and lies below the level of the occlusal surface of the last molar. It is not possible to trace the relationships of the different bones forming the pterygoid process since all sutures are

PLATE 19

Rytiodus zeltenensis sp. nov.

M19101a : ventral view of skull

(see Plate 22 for dentition)

FIGURE 30

Drawing of Plate 19

(see Figure 34 for dentition)

PLATE 19

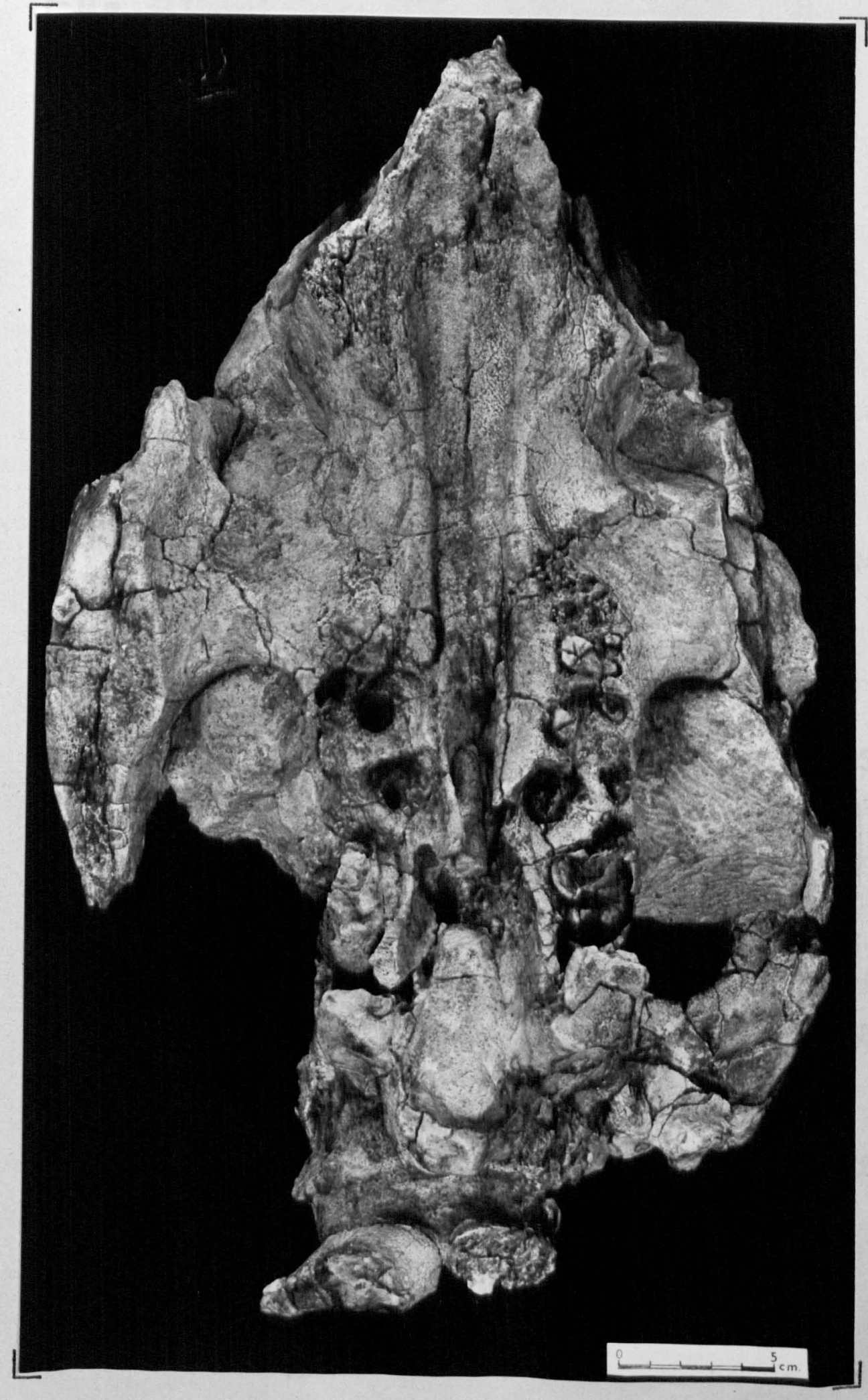
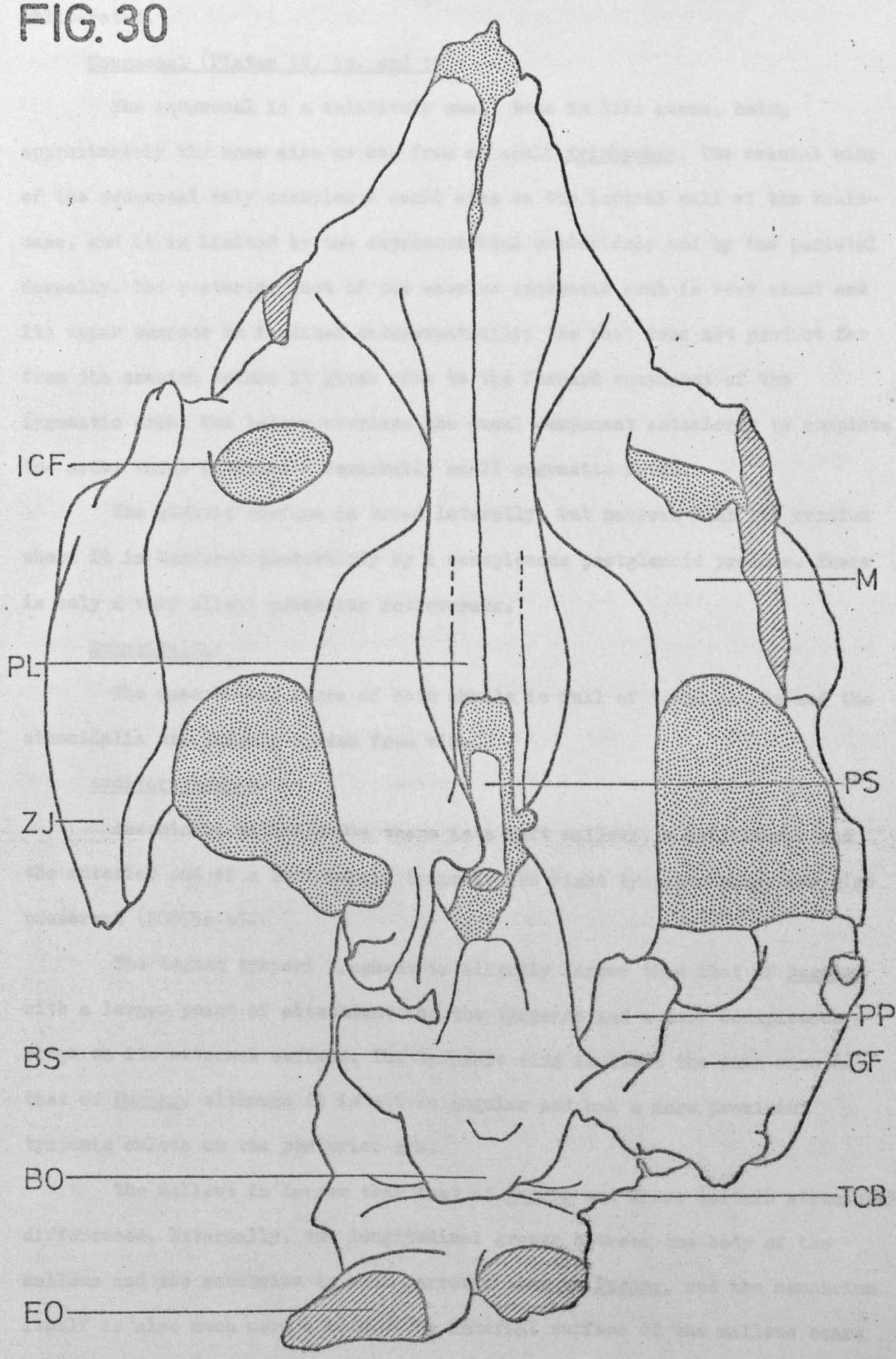


FIG. 30



obliterated.

Squamosal (Plates 14, 18, and 19):

The squamosal is a relatively small bone in this genus, being approximately the same size as one from an adult Trichechus. The cranial wing of the squamosal only occupies a small area on the lateral wall of the braincase, and it is limited by the supraoccipital posteriorly and by the parietal dorsally. The posterior root of the massive zygomatic arch is very stout and its upper surface is inclined anteroventrally; the root does not project far from the cranium before it gives rise to the forward component of the zygomatic arch. The latter overlaps the jugal component anteriorly to complete the arch, which encloses a remarkably small zygomatic fossa.

The glenoid surface is broad laterally, but narrows near the cranium where it is bordered posteriorly by a conspicuous postglenoid process. There is only a very slight processus retroversus.

Ethmoidalia:

The mesorostral fossa of both skulls is full of tough matrix and the ethmoidalia are largely hidden from view.

Auditory region:

Associated with M19101a there is a left malleus, a left incus, and the anterior end of a left tegmen tympani. Two right tympanic rings are also preserved (20855a-b).

The tegmen tympani fragment is slightly larger than that of Dugong, with a larger point of attachment for the tympanic and a more conspicuous ridge on its external surface. The tympanic ring is about the same size as that of Dugong, although it is not so angular and has a more prominent tympanic sulcus on the posterior arm.

The malleus is larger than that of Dugong and shows certain structural differences. Externally, the longitudinal groove between the body of the malleus and the manubrium is much narrower than in Dugong, and the manubrium itself is also much more slender. The internal surface of the malleus bears only two facets for the incus (as in Hydrodamalis) instead of the three facets

found on the malleus of Trichechus, Halitherium, Dugong etc.. The incus is more robust than the corresponding bone in Dugong, and has two subequal facets for articulation with the malleus.

Cranial cavity and endocranial cast (Plate 19; Figure 31):

What remains of the cranial cavity is reminiscent of the corresponding vacuity in Dugong. The lateral walls, posterior wall, and floor of the brain-case are extensively broken, but the roof is fairly intact. The falx cerebri and tentorium cerebelli are both present on the internal surface of the parietal, but neither of them is very prominent. The falx is only manifest on the posterior part of the roof (in Dugong it extends for the whole length) and the tentorium is only slightly developed and just reaches the lateral walls of the brain-case (it is absent in Dugong). A large boss is produced at the junction of the tentorium and the falx.

Natural endocranial casts were removed from both skulls, that from M19101a being the more complete one. The casts show that the olfactory lobes were quite large and were ovoid in shape. The cerebral region is very large and accounts for the majority of the endocranial cast in terms of volume. The two cerebral hemispheres are separated posteriorly by the falx and there is some indication of a very indistinct Sylvian sulcus. The cerebellar region is compressed anteroposteriorly and is not markedly separated from the cerebral region. From the shape of the cast of the spinal cord it appears that the foramen magnum was triangular in section with an acute apex.

Two pairs of nerve exits are preserved on the cast from M19101a. The roots of the optic nerves (II) are prominent, but the optic chiasma is not distinguishable. The complex of cranial nerves III, IV, V, and VI, leading to the sphenorbital canal, is also evident on either side of a broad, shallow depression that was made by the basisphenoid.

Mandible (Plate 20):

The lower jaw of this sirenian is represented by a single specimen (20856) consisting of the posterior region of a left mandibular ramus containing an

FIGURE 31

Rytiodus zeltenensis sp. nov.

M19101a

A : left lateral view of endocranial cast

B : dorsal view of endocranial cast

C : ventral view of endocranial cast

$\times\frac{2}{3}$

FIG. 31

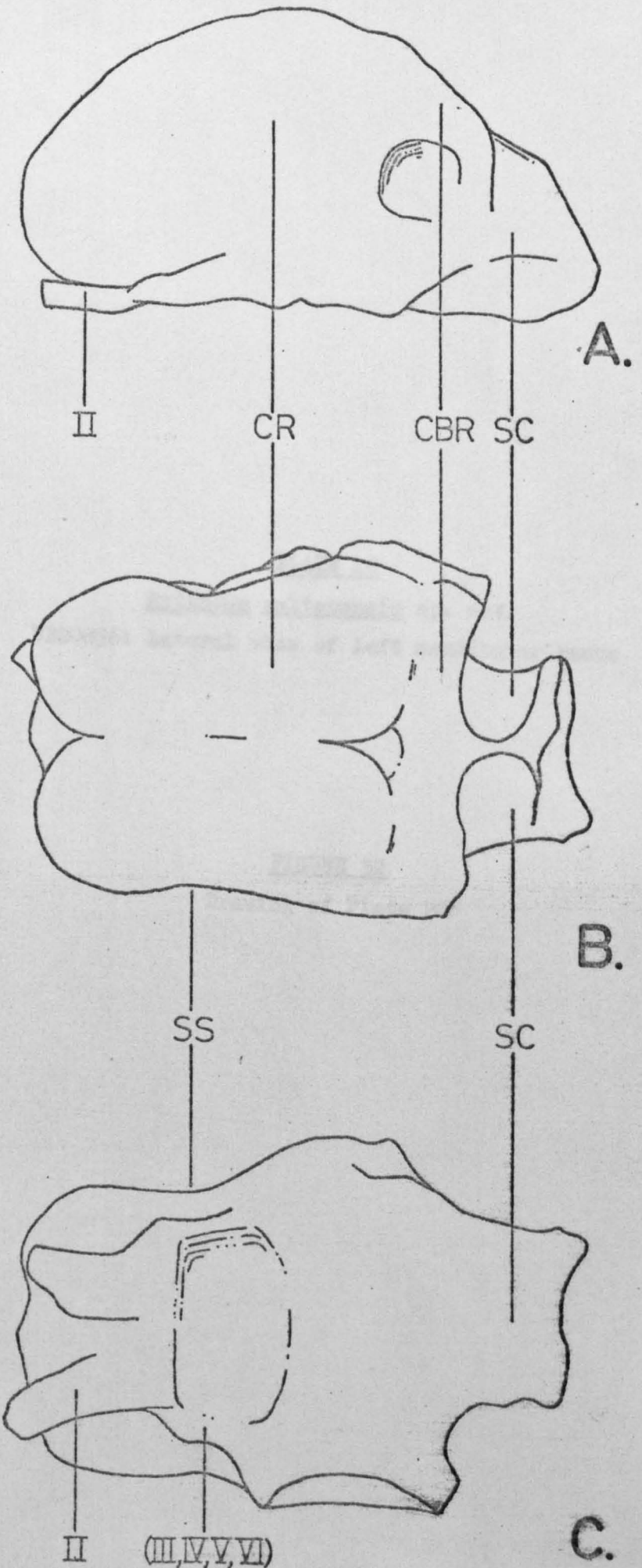


PLATE 20

Rytiodus zeltenensis sp. nov.

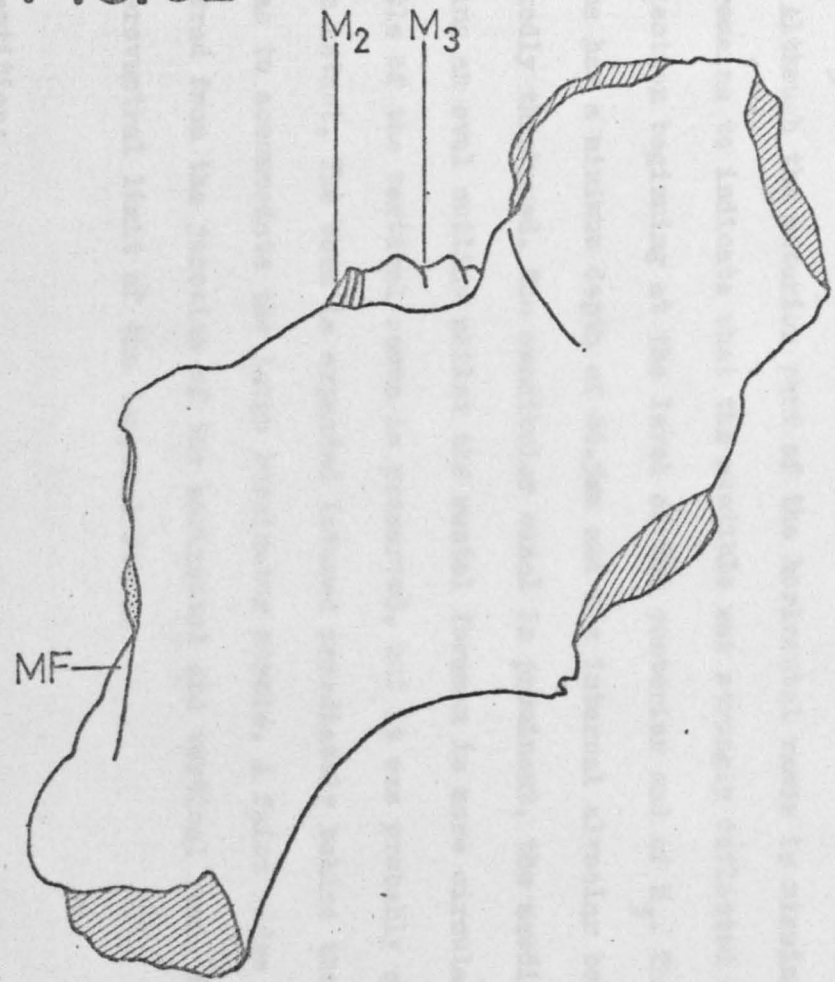
UB20856: lateral view of left mandibular ramus

FIGURE 32

Drawing of Plate 20

PLATE 20

FIG. 32



intact M_3.

Although the anterior part of the horizontal ramus is missing, enough of it remains to indicate that the mandible was strongly deflected - the deflection beginning at the level of the posterior end of M_3. The horizontal ramus has a minimum depth of 86.5mm and its internal alveolar border is markedly thickened. The mandibular canal is prominent, the mandibular foramen having an oval outline whilst the mental foramen is more circular. Very little of the vertical ramus is preserved, but it was probably quite large when intact. The bone is expanded laterad immediately behind the last molar so as to accommodate the large buccinator muscle. A faint ridge runs postero-ventrad from the junction of the horizontal and vertical rami, forming the anteroventral limit of the temporal fossa.

Dentition:

Apart from the spectacular upper incisors the dentition is poorly represented, since only three cheek teeth are intact and much of the alveolar region is broken away. The maxillae of 20853a only exhibit the anterior alveoli and even these are obliterated; the maxillae of M19101a are better preserved and contain the remains of two teeth still in their sockets. The mandible, 20856, contains a complete M_3, but the rest of the tooth row is very fragmentary.

Dental formula (Plates 22 and 23):

The alveoli for the upper cheek teeth are present on M19101a, but are difficult to elucidate because of their broken walls. The tooth row of this specimen does not yet contain its full complement of cheek teeth because the third molar has not fully erupted and is still partially within the dental capsule. It appears that a maximum of four teeth could have been present on each side at any one time (on M19101a we are witnessing the loss of the most anterior cheek tooth and its replacement by a new tooth at the posterior end of the tooth row) (see Plate 22).

The left mandibular ramus attributed to this species is broken and

thus the precise dental formula cannot be determined. However, the mandible contains the only complete tooth - a large M_3. Anterior to this tooth there are the remains of the M_2; a third, much smaller, molar was probably present in front of the M_2, but the shape of the alveolar border precludes the existence of any other mandibular cheek teeth.

From the above information it is possible to present an incomplete dental formula of:

$$I\ \frac{1}{?},\ C\ \frac{0}{?},\ P\ \frac{2}{0},\ M\ \frac{3}{2 \text{ or } 3}$$

Teeth:

The upper teeth are represented by a pair of tusk-like incisors, a very worn P^4, and a broken M^3. The lower teeth are completely absent except for an intact M_3.

Incisors (Plates 16 and 21):

One of the most noticeable features of 20853a is the presence of a pair of massive incisor tusks in the upper jaw. These tusks are unusual because they are laterally compressed and not cylindrical like the tusks of the majority of other sirenians. The alveolus of each tusk is large and opens anteroventrally. The size of the two alveoli cannot be accurately determined because their walls are badly damaged. The tusks are large, and have suffered a conspicuous lateral compression that has produced two very narrow teeth. A cross-section of a tusk shows that it is thicker on the labial edge than it is on the lingual, because of a slight shoulder that runs the length of its external surface (see Plate 21). The pulp cavity is narrow and is surrounded by a thick layer of dentine; the enamel occurs as a very thin external layer and very little of it remains on the material available. An unusual feature concerning the enamel is that it is raised into a series of parallel ridges that appear to have extended from the root to the tip of the tusk (see Lartet, 1866). Few measurements are possible on the incisors, but the left tusk of 20853a was at least 77.4mm deep and 25mm wide.

Premolars (Plate 22):

At the anterior end of the upper tooth row of M19101a there is a

PLATE 21

Rytiodus seltenensis sp. nov.

UB20853a: incisor tusks

FIGURE 33

Drawing of Plate 21

PLATE 21

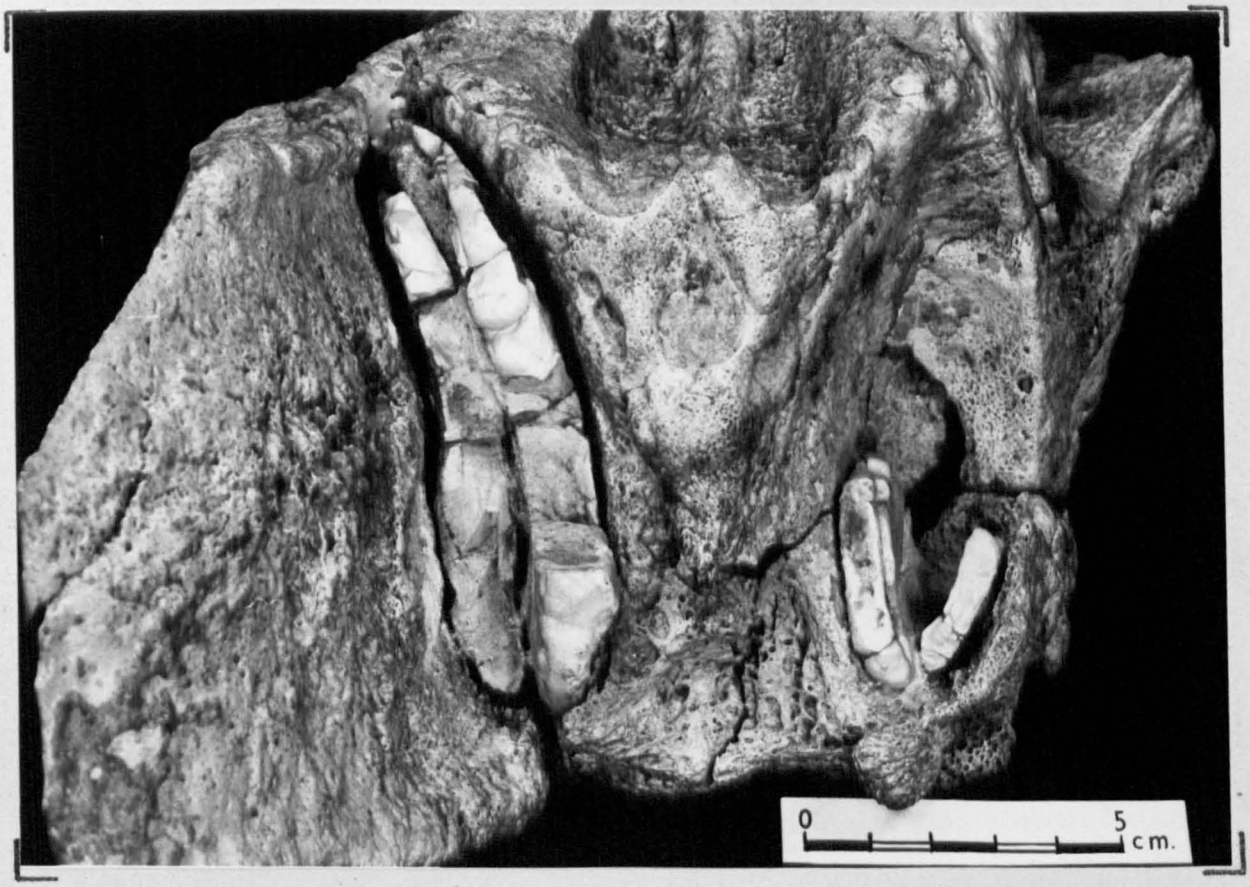


FIG. 33

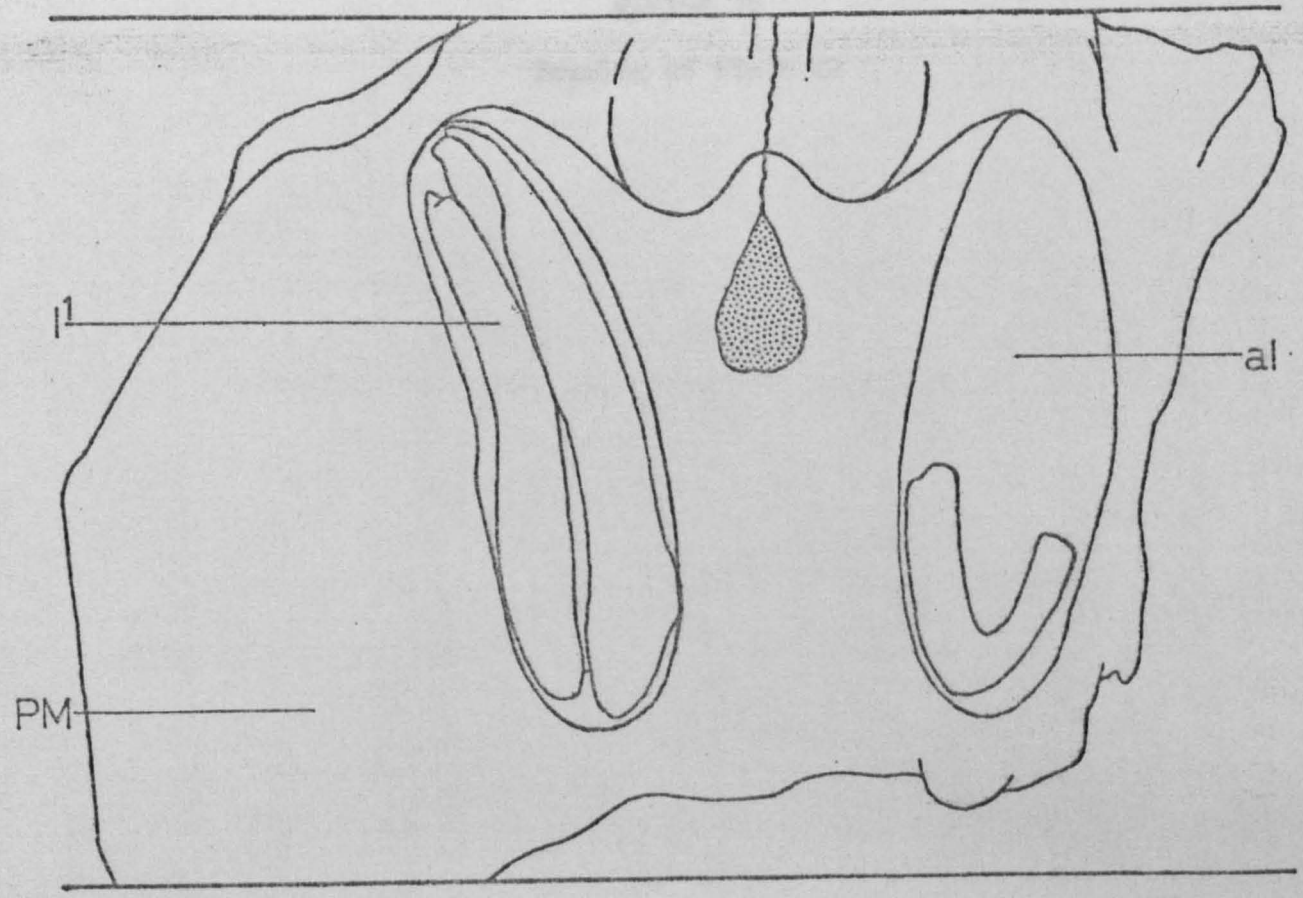


PLATE 22

Rytiodus zeltenensis sp. nov.
M19101a: maxillary dentition

FIGURE 34

Drawing of Plate 22

PLATE 22

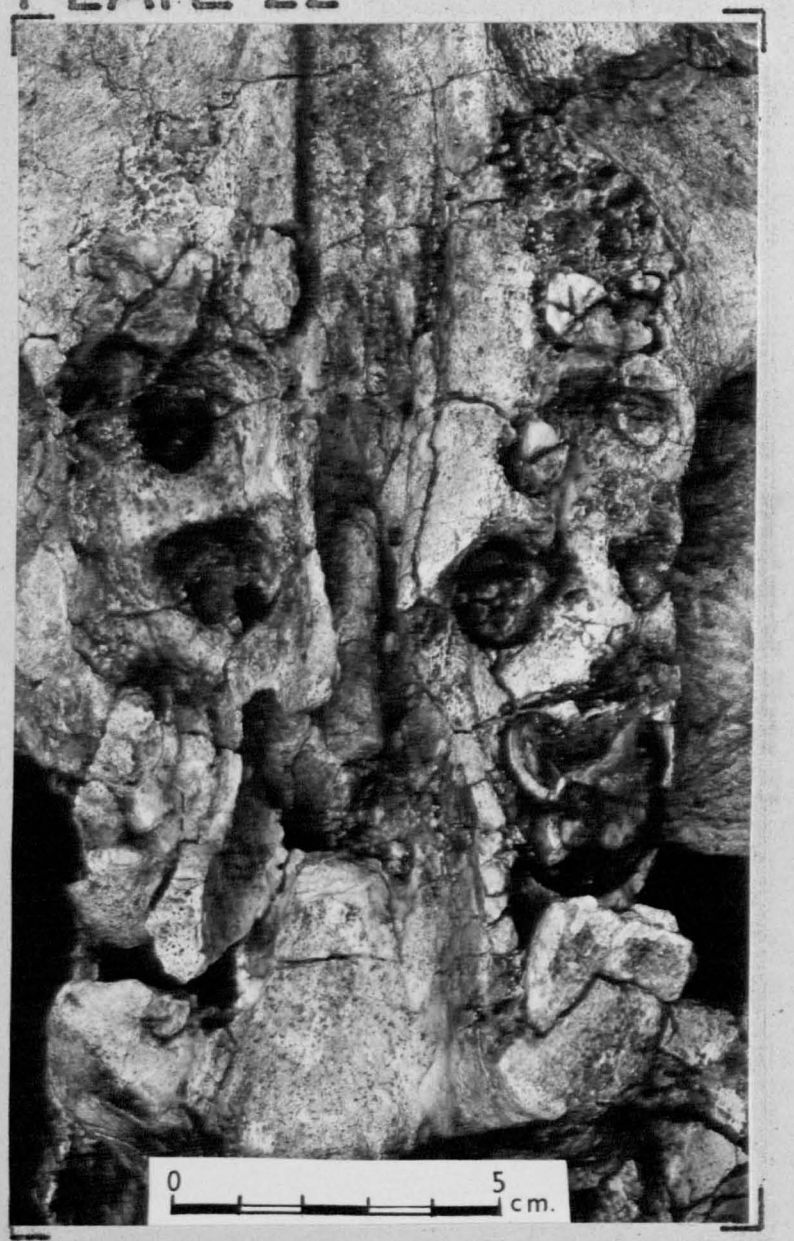


FIG. 34

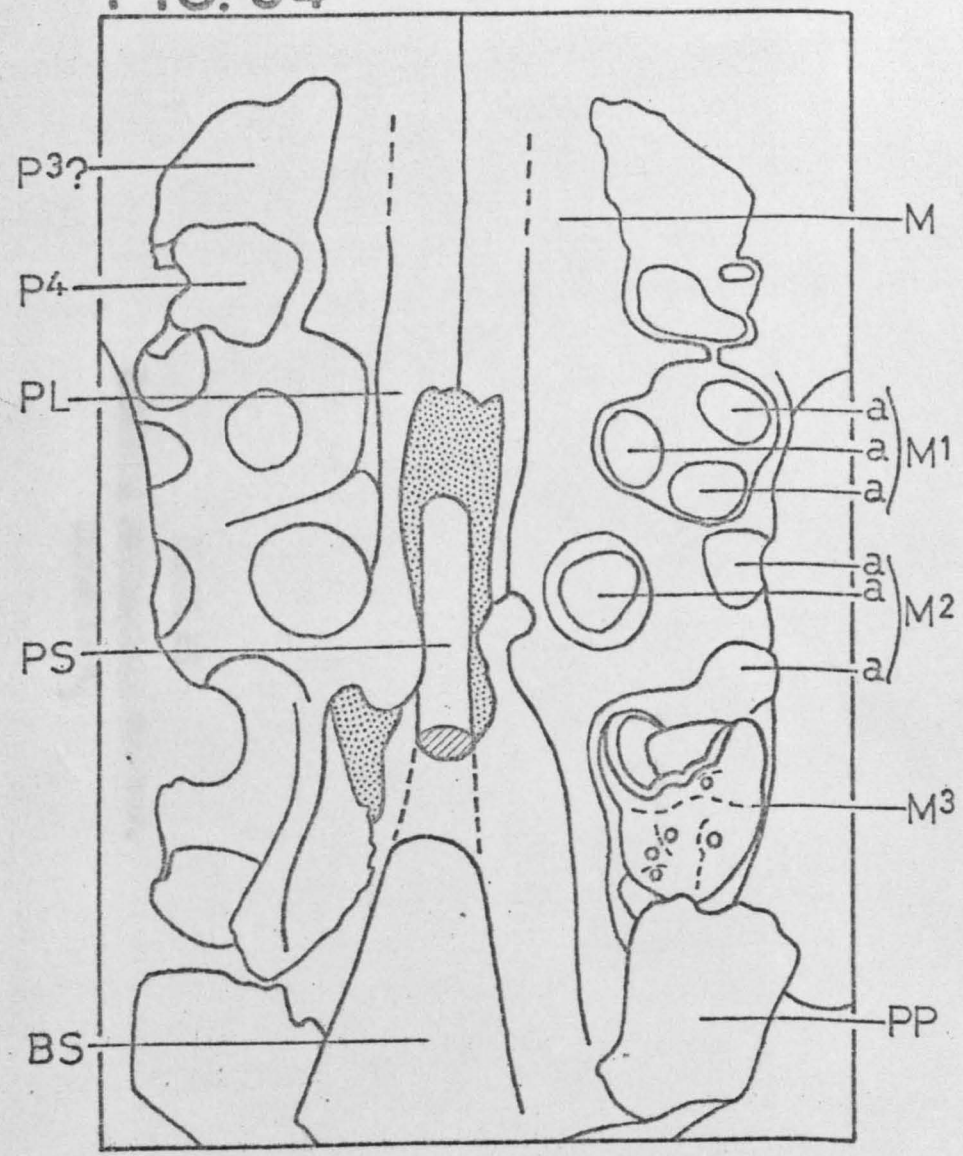


PLATE 23

Rytiodus zeltenensis sp. nov.

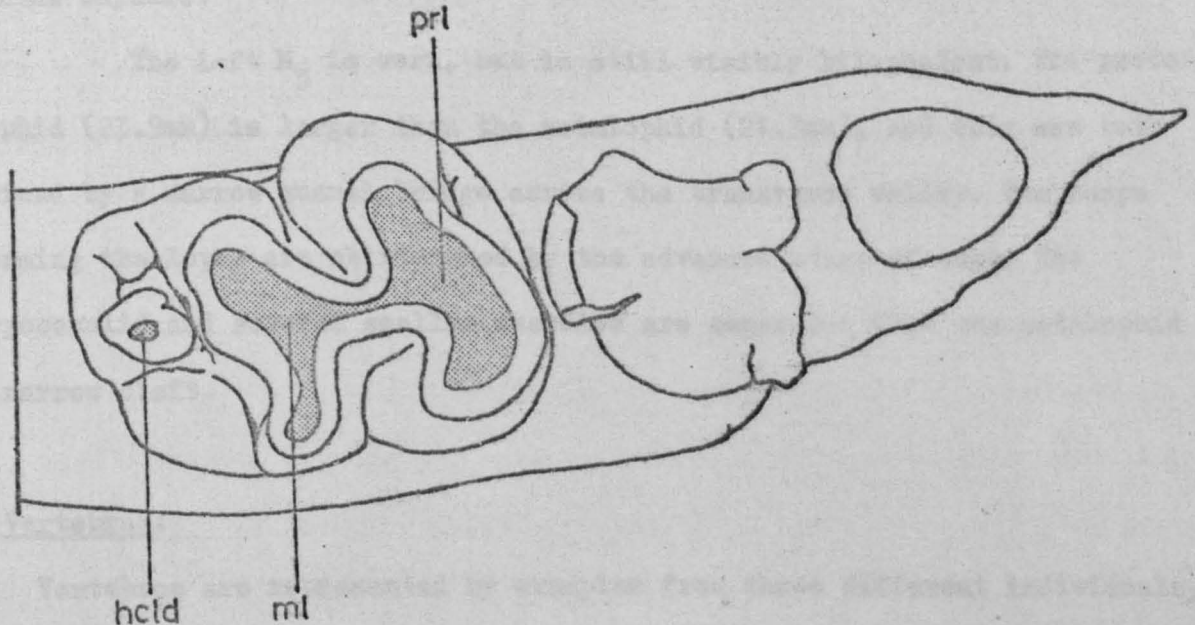
UB20856: M_3

FIGURE 35

Drawing of Plate 23

PLATE 23

FIG. 35



triangular area of cancellous bone, which indicates that a very worn tooth (P^3) has been discarded to make way for the last molar. Traces of the roots show that P^3 was tri-rooted. The worn vestiges of both P^4's are present and each has two slender, external roots and one, possibly two, similar internal roots. The occlusal surface of P^4 has been flattened by prolonged wear, and no trace of lophodonty remains. However, the external margin of the crown is indented about midway along its length, showing that the tooth was probably bilophodont when unworn.

Molars (Plates 14, 20, 22, and 23):

The first and second upper molars are missing, but both had a large internal root and two smaller, external ones.

The third upper molar is not completely visible on the left side of M19101a and it is impossible to see how many roots it has. It is an elongated tooth that is widest (23.8mm+) across the protoloph. Most of the protoloph is broken away, but it was formed from a number of distinct cusps. A deep transverse valley separates the protoloph from the metaloph, but it is partly obstructed by the metaconule. The metaloph is complete and unworn, and is formed from three large cusps (metacone, metaconule, and hypocone). A series of cuspules behind the metaloph assume the appearance of a curved third loph (tritoloph ?), but this part of the tooth is hidden by the walls of the dental capsule.

The left M_3 is worn, but is still visibly bilophodont. The protolophid (23.9mm) is larger than the metalophid (21.3mm), and they are both joined by a narrow enamel bridge across the transverse valley. The cusps forming the lophs are obliterated by the advanced stage of wear. The hypoconulid and several smaller cuspules are separated from the metalophid by a narrow cleft.

Vertebrae:

Vertebrae are represented by examples from three different individuals, and include specimens of both the cervical and thoracic series.

Cervical vertebrae:

Cervical vertebrae from two individuals give an almost complete view of this series, although the atlas vertebra (1st. cervical) is missing in both cases. Three vertebrae (axis, 3rd. cervical, and 7th. cervical) are associated with 20853a, whilst four more (4th., 5th., 6th., and 7th. cervicals) belong to M19101a.

Axis (2nd. cervical vertebra) (Plates 24 and 25):

The axis is well preserved and is fused with the 3rd. cervical to form a compact unit (20853b). The odontoid process is a stout, cylindrical structure with a flanged, circular depression on its anteroventral surface that would articulate with the ventral arch of the atlas. Small, rounded depressions for the ligamentum dentis occur on either side of the process, and lateral to each of these is a large anterior articular facet. The centrum is rectangular and has a concave posterior surface. Only the left diapophysis is intact and it is short, compressed, and directed posteriorly. The postzygapophyses are situated about halfway up the pedicles of the neural arch, and in this specimen they are not united with the prezygapophyses of the 3rd. cervical. The neural arch is massive, mainly because its dorsal moiety is intimately fused with the arch of the 3rd. cervical. The neural canal is triangular in shape and is higher than broad.

Petit (1928) noted four different degrees of fusion between the axis and the 3rd. cervical in Trichechus; the stage of fusion in 20853b corresponds to Petit's second degree because the zygapophyses of the two vertebrae have not yet united.

3rd.-7th. cervical vertebrae

The rest of the cervical vertebrae are very compressed antero-posteriorly and they are all basically very similar. The 3rd. cervical is the best preserved example and will be used as a model for the description of the others. The anterior surface of the thin, spongiose centrum is convex, forming an intimate articulation with the centrum of the axis. The diapophyses and parapophyses are short and thin, and they do not meet laterally to surround the vertebrarterial foramen. The pre- and postzygapophyses

PLATE 24

Rytiodus zeltenensis sp. nov.

UB20853b : anterior view of axis vertebra

PLATE 25

Rytiodus zeltenensis sp. nov.

UB20853b : left lateral view of axis vertebra

FIGURE 36

A : Drawing of Plate 24

B : Drawing of Plate 25

PLATE 24

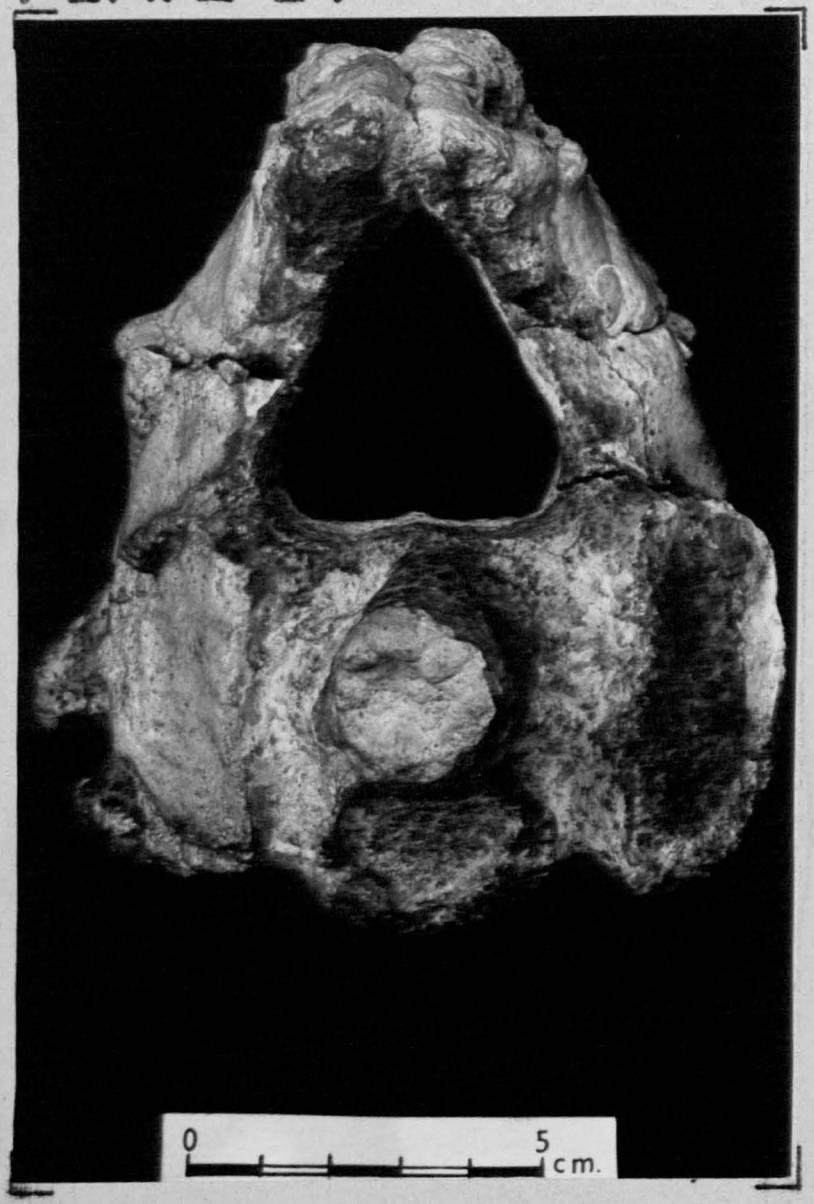


PLATE 25

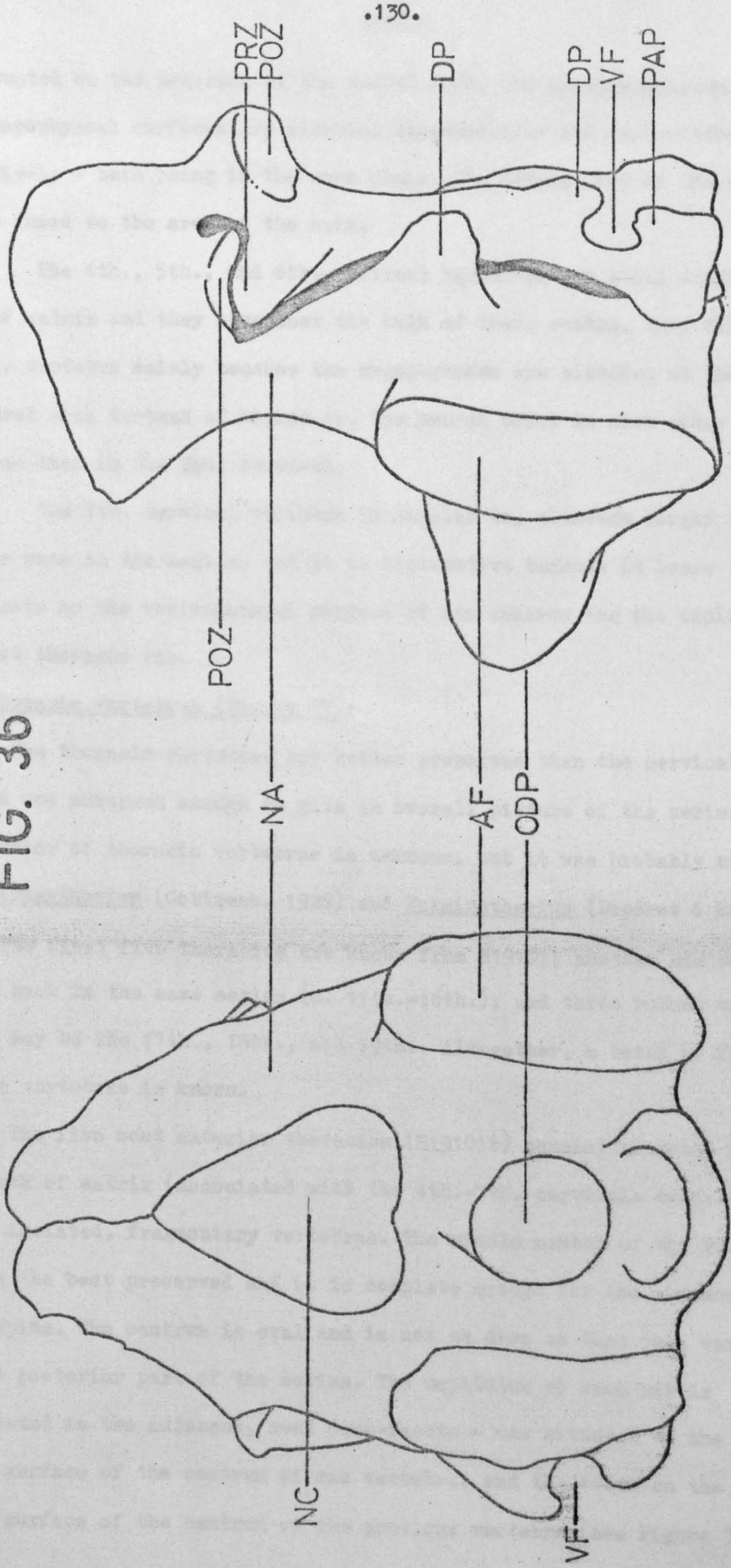


FIG. 36

are situated on the pedicles of the neural arch; the prezygapophyseal and postzygapophyseal surfaces are directed dorsomedially and ventrolaterally respectively - both being in the same plane. The dorsal part of the neural arch is fused to the arch of the axis.

The 4th., 5th., and 6th. cervical vertebrae are still enclosed in a block of matrix and they have lost the bulk of their centra. They differ from the 3rd. vertebra mainly because the zygapophyses are situated at the base of the neural arch instead of higher up. The neural canal is also wider in these vertebrae than in the 3rd. cervical.

The 7th. cervical vertebra is similar to, although larger than, the previous ones in the series, and it is distinctive because it bears two deep demi-facets on the ventrolateral corners of its centrum for the capitulum of the first thoracic rib.

Thoracic vertebrae (Figure 37):

The thoracic vertebrae are better preserved than the cervicals, but they are not numerous enough to give an overall picture of the series. The total number of thoracic vertebrae is unknown, but it was probably nineteen as in Metaxytherium (Cottreau, 1928) and Felsinotherium (Depéret & Roman, 1920). The first five thoracics are known from M19101; another six come from further back in the same series (c. 11th.-16th.); and three robust vertebrae (20857) may be the 17th., 18th., and 19th.. Altogether, a total of fourteen thoracic vertebrae is known.

The five most anterior thoracics (M19101b) consist of three vertebrae in a block of matrix (associated with the 4th.-7th. cervicals described above) and two isolated, fragmentary vertebrae. The middle member of the block of three is the best preserved and it is complete except for the absence of its neural spine. The centrum is oval and is not as deep as that on a vertebra from the posterior part of the series. The capitulum of each rib is accommodated in two adjacent, oval demi-facets - one situated on the antero-lateral surface of the centrum of one vertebra, and the other on the postero-lateral surface of the centrum of the previous vertebra (see Figure 37A). The

FIGURE 37

Rytiodus zeltenensis sp. nov.

M19101b

A': anterior view of anterior thoracic vertebra

A": left lateral view of anterior thoracic vertebra

M19101c

B': anterior view of posterior thoracic vertebra

B": left lateral view of posterior thoracic vertebra

$\times\frac{2}{3}$

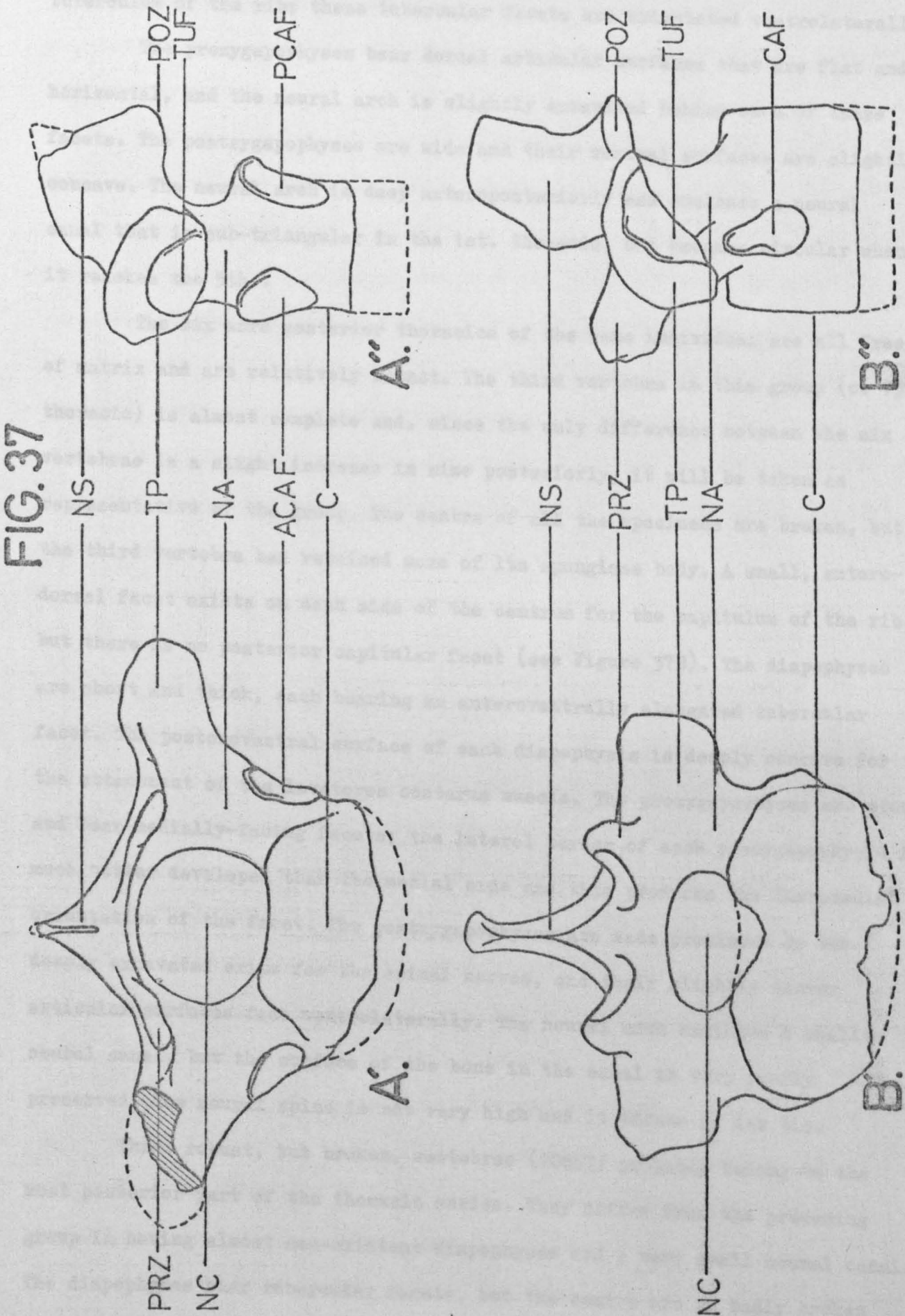


FIG. 37
NS
TP
NA
ACAF
C
POZ
TUF
PCAF
PRZ
NC
A'
A''
NS
PRZ
TP
NA
C
POZ
TUF
CAF
NC
B'
B''

diapophyses are long and slender, terminating in an oval depression for the tuberculum of the rib; these tubercular facets are orientated ventrolaterally.

The prezygapophyses bear dorsal articular surfaces that are flat and horizontal, and the neural arch is slightly excavated behind each of these facets. The postzygapophyses are wide and their ventral surfaces are slightly concave. The neural arch is deep anteroposteriorly and encloses a neural canal that is sub-triangular in the 1st. thoracic, but becomes circular when it reaches the 5th..

The six more posterior thoracics of the same individual are all free of matrix and are relatively intact. The third vertebra in this group (c. 13th. thoracic) is almost complete and, since the only difference between the six vertebrae is a slight increase in size posteriorly, it will be taken as representative of the group. The centra of all the specimens are broken, but the third vertebra has retained more of its spongiose body. A small, antero-dorsal facet exists on each side of the centrum for the capitulum of the rib, but there is no posterior capitular facet (see Figure 37B). The diapophyses are short and thick, each bearing an anteroventrally elongated tubercular facet. The posteroventral surface of each diapophysis is deeply concave for the attachment of the levatores costarum muscle. The prezygapophyses are stout and bear medially-facing facets; the lateral border of each prezygapophysis is much better developed than the medial side and this produces the dorsomedial orientation of the facet. The postzygapophyses are made prominent by the deeply excavated exits for the spinal nerves, and their slightly convex articular surfaces face ventrolaterally. The neural arch encloses a shallow neural canal, but the surface of the bone in the canal is very poorly preserved. The neural spine is not very high and it widens at its tip.

Three robust, but broken, vertebrae (20857) probably belong to the most posterior part of the thoracic series. They differ from the preceding group in having almost non-existent diapophyses and a very small neural canal. The diapophyses bear tubercular facets, but the centra are so badly broken that capitular facets cannot be identified.

Ribs:

The ribs can be divided into two groups; a group associated with the anterior thoracic vertebrae, and another group associated with the posterior thoracic vertebrae.

The anterior ribs are characterized by having the capitulum joined to the shaft by a prominent neck. On the capitulum the anterior articular surface is smaller than the posterior, but both are convex. The neck is oval in section. The tuberculum is at the base of the neck and bears a flat, oval articular surface. The proximal end of the shaft has a D-shaped cross-section.

The posterior ribs differ from the anterior ones in having no neck and confluent capitular and tubercular surfaces. The tubercular surface is elongated and is widest dorsally. The shaft of the rib is oval in section and has a wide groove on its posterior margin. All of the rib fragments exhibit pachyostosis.

Comparison and discussion:

The unusual sirenian genus Rytiodus was originally described by Lartet (1866) on the basis of some extraordinary teeth from a quarry at Bournic in the Aquitaine Basin, France. Apart from some skull and rib fragments associated with these teeth, the anatomy of the type species, Rytiodus capgrandi, was unknown until Delfortrie (1880) published a description of a broken skull and an atlas vertebra from Saint-Morillon, also in the Aquitaine Basin. The strata from which the two specimens came have been shown to be synchronous with the "falun de Bazas" (Tournouër, 1866; Delfortrie, 1880), which places them within the Aquitanian (Lower Miocene). This new find of the genus in the Burdigalian deposits of central Libya increases both its stratigraphical and geographical range.

Delfortrie's account of the skull of Rytiodus capgrandi is very short, but, apart from one serious error, it is reasonably accurate. A look at Delfortrie's

life-size reconstruction of the skull (1880, plate V) reveals that he mounted the broken anterior part of the rostrum in a horizontal position, so that it gives the impression of a long, undeflected premaxillary region. This restoration has led all subsequent authors to believe that Rytiodus differs from all other dugongids in having a straight rostrum - a feature that up until now has been used as a generic character. The Libyan material reveals that the rostrum was in fact very strongly deflected and that Delfortrie was misled as to its shape because part of it was missing from his specimen. Rytiodus is therefore closer to the typical dugongids than was previously believed.

It is necessary to compare Rytiodus zeltenensis with R. capgrandi, and with the genera Halitherium, Anomotherium, Metaxytherium, and Caribosiren, so that its position in the sirenian evolutionary sequence can be determined.

The abbreviated anatomical description of R. capgrandi places emphasis on parts of the skull that are missing from both specimens of R. zeltenensis, and this means that a detailed comparison of the two species is almost impossible. However, both species show evidence of a close relationship - especially in the presence of a pair of distinctive incisor tusks. The differences between R. capgrandi and R. zeltenensis can best be listed:

TABLE 6

R. capgrandi	R. zeltenensis
1. Premaxillary rami do not reach the nasals.	Premaxillary rami abut against anterior margins of nasals.
2. Rounded lacrimal.	Triangular lacrimal.
3. No median crest on occipital.	Prominent median crest on upper part of occipital.
4. Circular foramen magnum.	Triangular foramen magnum.

These few differences between the two species contrast with the great similarity between the teeth of R. capgrandi illustrated by Delfortrie (1880, plate VIII) and the few known teeth of R. zeltenensis. The differences may be due to intraspecific variation and subsequent material may prove that the French and Libyan forms are conspecific; however, the degree of anatomical

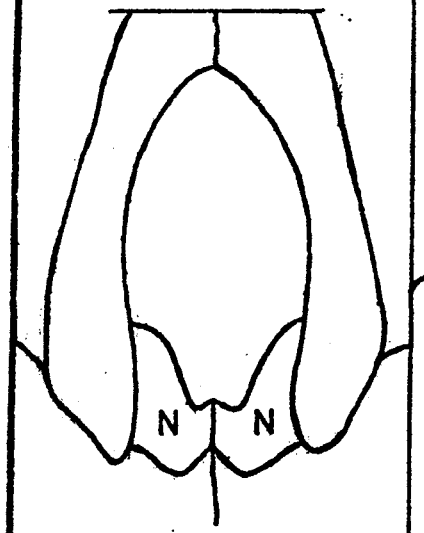
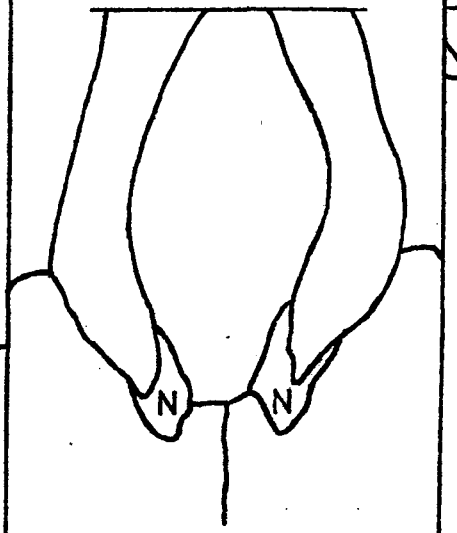
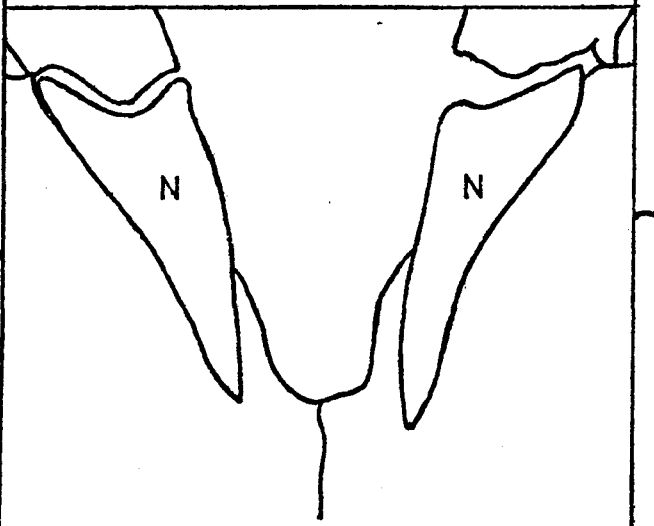
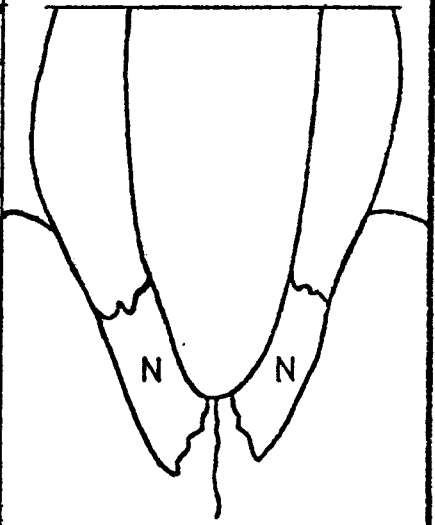
variation, the geographical separation, and the different geological ages have been taken as important enough to warrant the erection of a new taxon.

The genera Halitherium, Anomotherium, and Metaxytherium are believed by Siegfried (1965) to form a continuous series through the Oligocene and the Miocene, although Anomotherium has some unusual features (such as the structure of M_3) that do not conveniently fit into the sequence. Halitherium is a well-known Oligocene genus that is characterized by H. schinzi Kaup; Anomotherium langewieschei Siegfried is based on a single, almost complete, skeleton from the uppermost Chattian (Upper Oligocene); and Metaxytherium is a Miocene genus that is best represented by M. medium (Desmarest). Halitherium and Metaxytherium are both found in the Old and New Worlds, but Anomotherium is restricted to the Old World.

The two features most commonly used to classify sirenians are the reduction in the number of teeth and the gradual decrease in size of the nasals. The dental formula and nasal configuration of Rytiodus show that it is at a similar evolutionary stage to Metaxytherium in these respects. These two Miocene genera have very reduced dentitions (Rytiodus retains two of its upper premolars whereas Metaxytherium has only one) and their nasals show certain similarities also (being separated by the frontals in the mid-line and being situated behind the premaxillary rami). Although the two genera are similar in these respects it is obvious that they are members of two distinct lineages, and that the parallels in their anatomy are due to convergence. Evidence for the two lineages includes the structure of the tusks, the shape of the meso-rostral fossa and surrounding bones, and the narrowness of the skull of Rytiodus.

The skull of Rytiodus also shows similarities to that of the tuskless sirenian Caribosiren turneri Reinhart from the San Sebastian Formation of Puerto Rico (Reinhart, 1959). The evidence available to Reinhart suggested that the San Sebastian Formation was Middle Oligocene in age, and more recent evidence (van den Bold, 1965) supports this date with a Late Oligocene age for the upper part of the same formation. Reinhart believed that Caribosiren

TABLE 7 Comparison of four dugongid genera

	Halitherium	Caribosiren	Rytiodus	Metaxytherium
1. dental formula	$\frac{1}{3}$ $\frac{0}{1}$ $\frac{4}{4}$ $\frac{3}{3}$	$\frac{0}{?}$ $\frac{0}{?}$ $\frac{2}{?}$ $\frac{3}{?}$	$\frac{1}{?}$ $\frac{0}{?}$ $\frac{2}{0}$ $\frac{3}{3}$	$\frac{1}{0}$ $\frac{0}{0}$ $\frac{1}{1}$ $\frac{3}{3}$
2. lacrimal bone	present	present	present	present
3. lacrimal duct	present	absent	absent	absent
4. nasal region (x1/2)				
5. age	Oligocene	Oligocene	Miocene	Miocene

showed similarities to Halitherium, Felsinotherium, and Dugong (i.e. the typical dugongids), but,apart from comparing the degree of tooth reduction, he did not look closely at Rytiodus. The greatest resemblance between Rytiodus and Caribosiren occurs in the shape of the premaxillae, nasals, and lacrimals - these two genera are the earliest dugongids to have lost the use of the lacrimal duct. The auditory region of Rytiodus, although very poorly preserved, is noticeably small in relation to the size of the rest of the skull; this feature was also commented upon by Reinhart when referring to Caribosiren. The post-canine dental formula of the upper jaw is identical in both genera, but the absence of incisor tusks in the unique specimen of Caribosiren (probably a sexual dimorphic character: see Chapter 4) is an important factor in distinguishing the two genera at present. The frontals of Caribosiren account for a much greater area of the skull roof than do those of Rytiodus, and the temporal crests of the former are limited to the parietals. Caribosiren is undoubtedly close to the branch of the sirenian evolutionary tree occupied by Rytiodus although its exact position needs to be carefully studied.

The unusual features of Rytiodus capgrandi justified it being placed in a new subfamily of the Dugongidae, the Rytiodinae, by Abel (1928), and the discovery of R. zeltenensis does not affect this assignment. The rytiodines broke away from the typical dugongid line before the appearance of the genus Metaxytherium, because R. capgrandi is already very advanced by the Aquitanian. They most likely originated from one of the Oligocene species of Halitherium and then unsuccessfully paralleled the main dugongid stock for a short time. Halitherium shows definite advances over the primitive Eocene sirenians, but still has potential for the radiation and divergence that it exhibits during the Early Miocene. It retains a full complement of relatively simple cheek teeth and has a marked deflection of the premaxillae that is absent in the Eocene genera. Halitherium possesses all of the typical sirenian features found in Rytiodus, but is still unspecialized enough to give rise to the Rytiodinae. Anomotherium and Metaxytherium are too specialized to have had anything to do with the ancestry of this subfamily.

Cope (1869) described a compressed incisor tusk from the Eocene of New Jersey as belonging to a new sirenian, Hemicaulodon effodiens, and he noted similarities between this tusk and those of Rytiodus capgrandi - viz. groove on external surface, ridges on dentine. Kellogg (1966) believed that this tusk actually came from Miocene deposits overlying the Eocene ones, and he also commented on its resemblance to the tusks of Rytiodus. The specimen has since been lost.

Subfamily METAXYTHERIINAE subfam. nov.

Diagnosis: Rostrum strongly deflected; nasals separated in mid-line by frontals. Incisor tusks present (in adult males only ?); cheek teeth enamelled; M^3 unreduced and complex.

Remarks: This subfamily contains the genera Caribosiren, Metaxytherium (= Halianassa), and Felsinotherium. It represents a shortened version of the Halianassinae (Reinhart, 1959), which included Caribosiren, Halianassa, Hesperosiren, and Felsinotherium.

Genus METAXYTHERIUM de Christol 1840

Synonymy: The complicated synonymies of Metaxytherium and Halianassa have been ably dealt with by Kellogg (1966). Since no reliable characters have been found that can differentiate these two genera, they are here united under the senior synonym, Metaxytherium.

Diagnosis: Smaller, less progressive, Miocene genus (see Remarks below).

Type species: Metaxytherium medium (Desmarest 1822); Miocene (Helvetian = Burdigalian-Langhian) of Main-et-Loire, France.

Included species:
- M. beaumonti de Christol 1844 (including M. studeri von Meyer 1887, M. krahuletzi Depéret 1895)
- M. manigaulti (Cope 1883)
- M. lovisatoi Capellini 1886
- M. meyeri Abel 1904

M. jordani Kellogg 1925
M. crataegensis (Simpson) 1932
M. allisoni Kilmer 1965
M. calvertense Kellogg 1966
M. ortegense Kellogg 1966

Distribution: Lower-Middle(?) Miocene (Burdigalian-Langhian?) of Europe;
Lower(?)-Upper Miocene of the Americas;
Lower Miocene (Burdigalian) of Africa.

Remarks: According to Simpson (1932), no single character can be relied on to separate all the species of Metaxytherium from all the species of Felsinotherium. Both genera share the same anatomical features, although the latter genus is thought to be more progressive in certain of these features. The accepted practice has been to place Miocene metaxytheriines in the genus Metaxytherium, and to place the larger Pliocene forms in Felsinotherium. The validity of these two genera is best left undecided until better transitional (i.e. Upper Miocene) forms are known.

Metaxytherium sp. indet.

Referred material:	Site	
UB 20858	64.18	nasal region
UB 20859	64.20	premaxillary symphysis

Age and locality: Lower Miocene (Burdigalian) of Gebel Zelten (28°-29° N., 19° 30'-20° 30' E.), Libya.

Remarks: These are the remains of a sirenian that is anatomically distinct from, and smaller than, Rytiodus zeltenensis.

Anatomical description:

Skull (Plate 26):

The larger of the two skull fragments, 20858, consists of the anterior half of a skull and shows parts of the premaxillae, maxillae, nasals, lacrimal, frontals, palatines, and ethmoidalia. The smaller fragment (20859) is from another individual and represents part of the symphysial region of a left premaxilla.

Premaxillae:

A large part of the premaxillary region is still attached to 20858. Each premaxillary ramus has an ovoid cross-section anteriorly, but becomes progressively flatter towards the naso-frontal region. The major part of each ramus is supported by the maxilla, although posteriorly it lies between the nasal and the supraorbital process of the frontal. The symphysial region is poorly preserved and the only indication of the presence of incisor tusks is the occurrence of two adjacent concavities on the broken anterior surfaces of the premaxillae (see Figure 38). These depressions represent the posterior walls of the incisor tusk alveoli. The dorsal part of the premaxillary symphysis (as represented by 20859) shows the rostrum to have been strongly deflected, and the surface of the interpremaxillary suture has an enlarged contact area that would strengthen the symphysis. The mesorostral fossa is narrow and oval, and therefore differs from the wide, double-arched fossa of Rytiodus zeltenensis.

Maxillae:

The maxillae are poorly preserved because, apart from a small piece attached to the right premaxilla, they are only intact on the palatal surface of 20858. On the right side the maxilla is curved dorsad to form the medial surface of the infraorbital canal and then expands laterad to support the premaxilla and make contact with the anterior edge of the supraorbital process of the frontal. The lateral wall of the infraorbital canal is broken, but its dorsal point of attachment is visible. A small palatine foramen can be seen.

Nasals:

These are small, thin bones that are separated in the mid-line by a forward extension of the frontals. Each nasal is tilted ventrolaterad - the pair forming an incomplete, pitched roof for the posterior part of the meso-rostral fossa. The nasals are separated from the supraorbital processes of the frontals by the interposition of the premaxillary rami, but they contact the frontals when the rami terminate. The naso-frontal sutures demarcate a narrow extension of the frontals that reaches the posterior margin of the mesorostral fossa between the nasals.

PLATE 26

Metaxytherium sp. indet.

UB20858 : nasal region

FIGURE 38

Drawing of Plate 26

PLATE 26

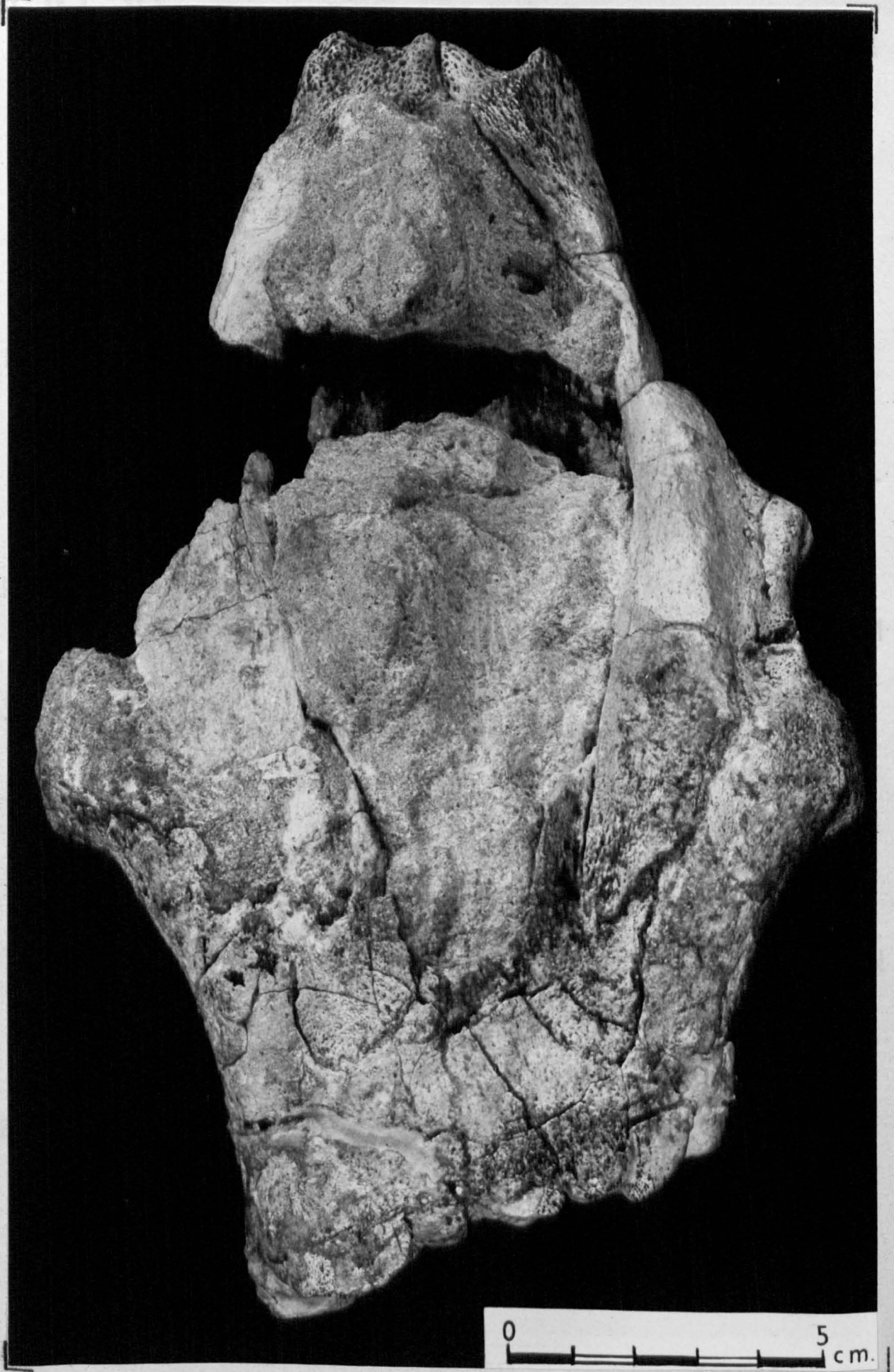


FIG. 38

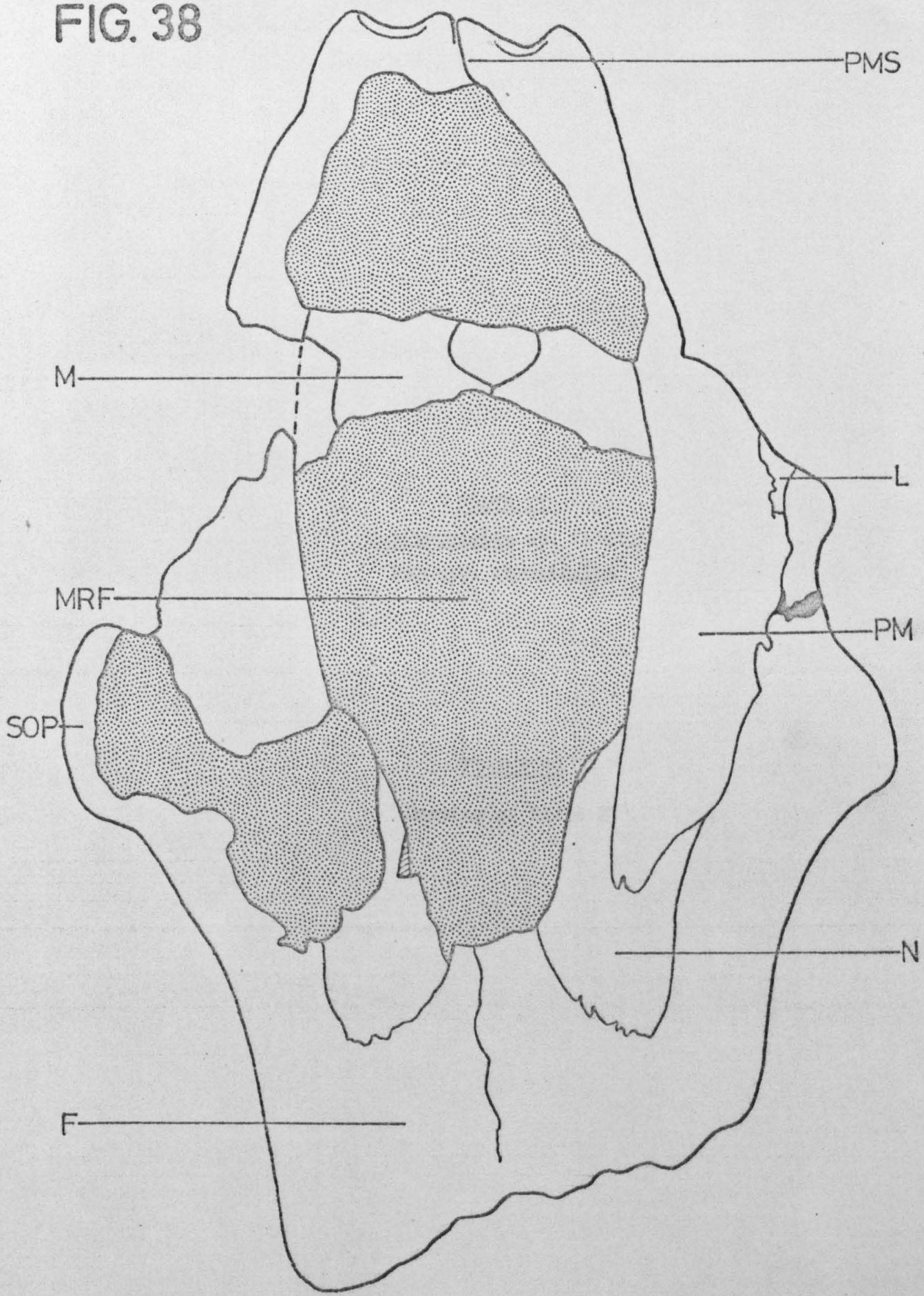


PLATE 27

Metaxytherium sp. indet.

UB20858: ethmoidalia

FIGURE 39

Drawing of Plate 27

PLATE 27

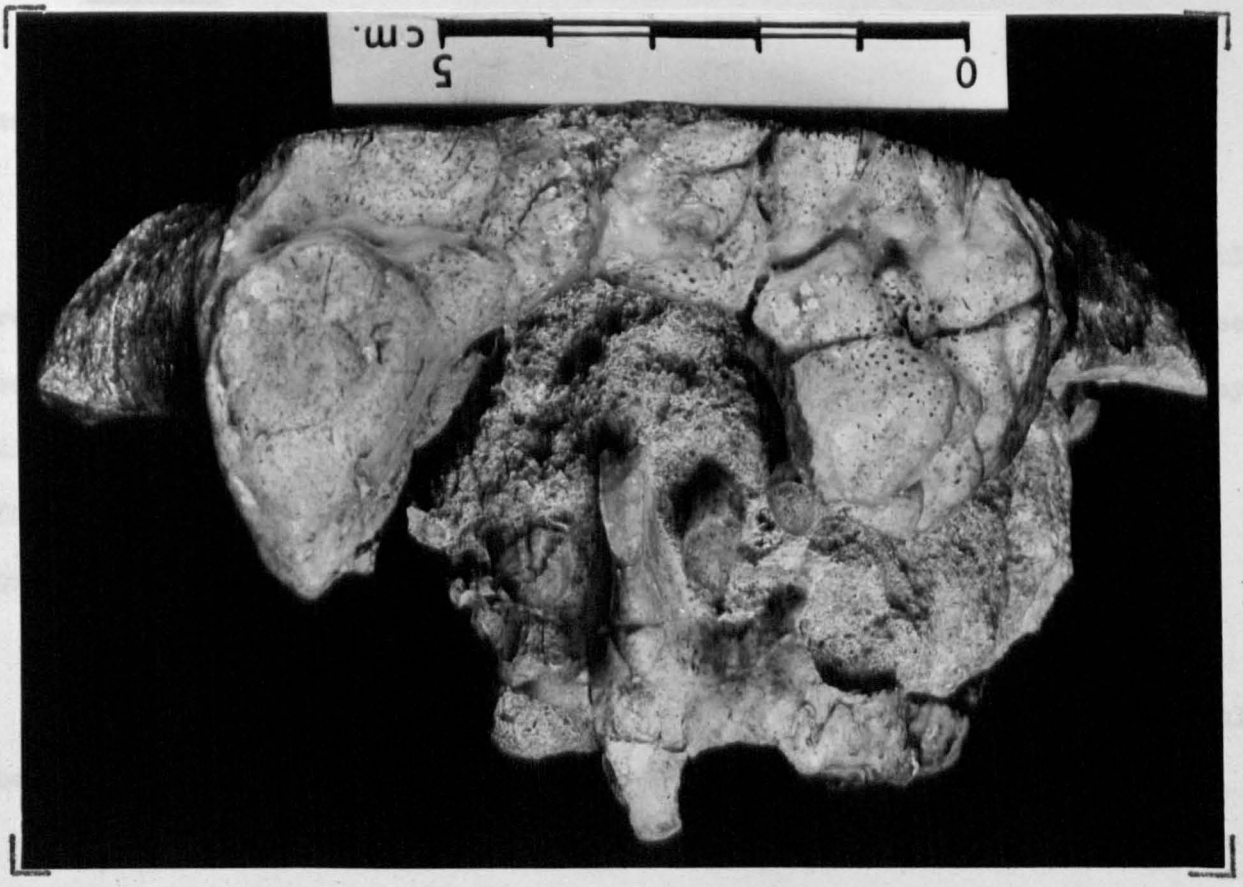
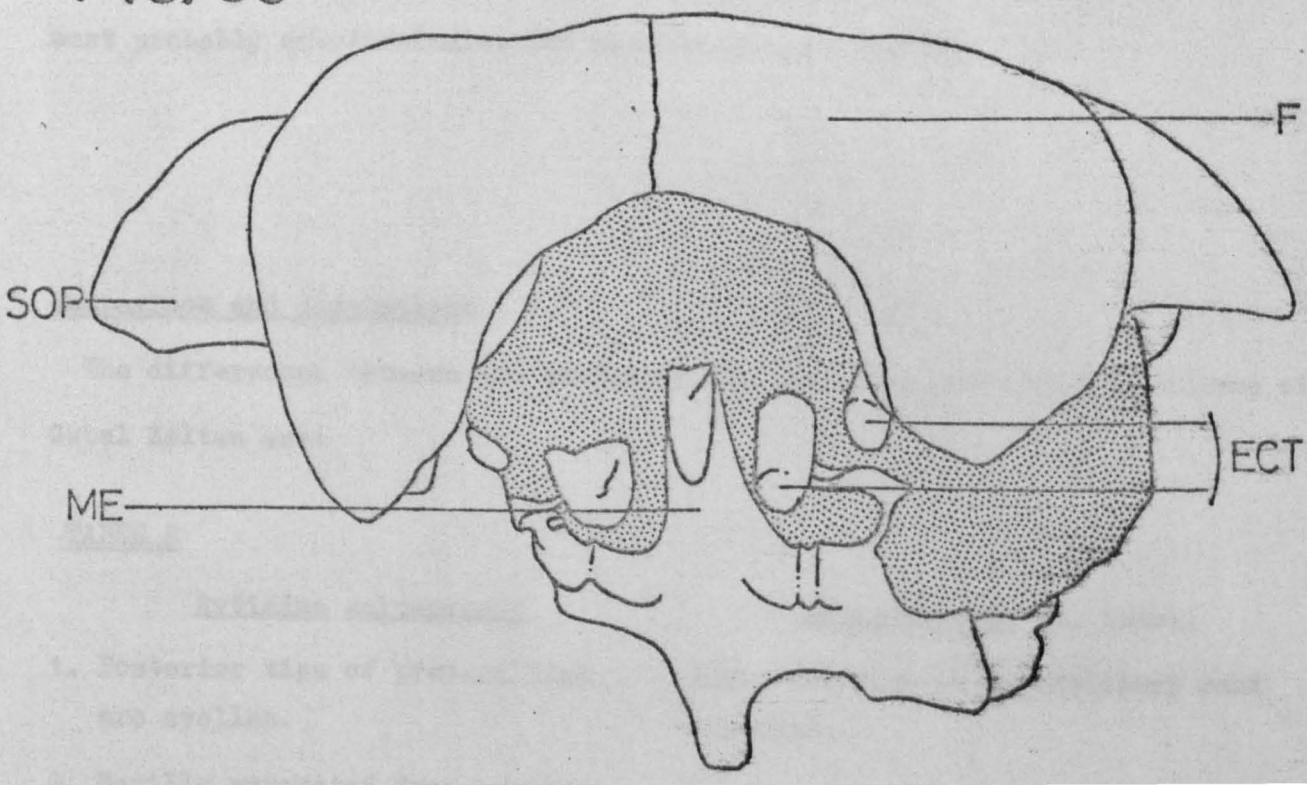


FIG. 39



Lacrimal:

A small fragment of the right lacrimal is wedged between the premaxillary ramus and the supraorbital process of the frontal on 20858.

Frontals:

The supraorbital processes of the frontals are intact, but very little remains of the cranial parts of these bones. The narrow supraorbital processes contact the maxillae anteriorly and the premaxillae and nasals medially; they then continue back beyond the tips of the premaxillary rami to enlarge and form part of the roof of the braincase. A forward extension of the frontals produces a truncated W-shaped suture with the nasals.

Palatines:

The palatines are indistinguishable from the maxillae, but they should be present because the anterior rim of the nasopharyngeal fossa is complete.

Ethmoidalia (Plate 27):

The structure of the ethmoid region can be seen in transverse section on the posterior surface of 20858. The nasal cavity is full of matrix, but the swollen tips of some of the turbinal bones can be detected protruding from it. Since only the extremities of the bones are visible it is impossible to identify them with any accuracy; however, the two pairs that can be seen are most probably ectoturbinals. The scrolls are not visible.

Comparison and discussion:

The differences between the skulls of the two sirenians from the Miocene of Gebel Zelten are:

TABLE 8

Rytiodus zeltenensis	*Metaxytherium* sp. indet.
1. Posterior tips of premaxillary are swollen.	Posterior tips of premaxillary rami are flat.
2. Maxilla separated from supraorbital process of frontal by lacrimal.	Maxilla contacts supraorbital process of frontal.

TABLE 8 (cont.)

	Rytiodus zeltenensis	Metaxytherium sp. indet.
3.	Nasals widest anteriorly.	Nasals widest posteriorly.
4.	Lateral edge of nasal in contact with supraorbital process of frontal for its entire length.	Lateral edge of nasal separated from supraorbital process of frontal for part of its length by the premaxillary ramus.
5.	Frontals contribute little to the formation of skull roof.	Frontals contribute significantly to the formation of skull roof.

Although very little of the skull of the second sirenian is known it is noticeable that it bears very little resemblance to the skull of Rytiodus. The dugongid affinities of this specimen are indicated by the evidence for a sharply deflected rostrum and incisor tusks. The only sirenian genus definitely known from the Aquitanian-Burdigalian, apart from the two species of Rytiodus, is Metaxytherium. The relatively large nasals that are separated in the mid-line by the frontals on 20858 suggest that this specimen is very close to the members of the latter genus. 20858 possesses no features that detract from this generic identification, but it is impossible to attempt an identification at species level.

This is the first record of Metaxytherium on the African continent, although it is widespread in the Miocene deposits of Europe.

Superfamily indet.

Sirenian A

Referred material:

	Site	
UB 20860a	68.01	fragments of at least 1 rib
UB 20860b	68.06	1 rib
UB 20860c	68.14	fragments of at least 6 ribs
UB 20860d	68.15	2 ribs
UB 20860e	68.16	1 rib

Age and locality: Upper Eocene (Priabonian) of Dor el Talha (25° 45' N., 18°-19° E.), Libya.

Remarks: Wight (1971) also recorded sirenian ribs from site 69.51, although he did not mention the single rib from site 68.06.

Anatomical description:

Sirenian ribs can be recognized by their short, stocky appearance and pronounced pachyostosis.

One or two of these ribs are almost complete, but none of them bear any trace of the capitulum or tuberculum. The two specimens from site 68.15 are the best for descriptive purposes; one being an almost intact bone, and the other showing much of the proximal region.

The proximal part of the near complete rib has an almost circular cross-section, but gradually the medial surface of the bone becomes flatter and it attains a D-shaped section near its middle. The flatness of the internal face is even more accentuated near the distal tip of the rib, and it ends as a well-rounded point. The width of the rib increases distally until it reaches a maximum about two-thirds of the way down the rib. The rest of the ribs are similar to the above, but differ in their degree of curvature.

The best preserved proximal region exhibits a sharp bend at its extremity that contrasts with the gentle curvature of the shaft. This bent portion probably bore the articular facets, but now no trace of them remains. The shaft of this rib has a more oval cross-section than the others.

Sirenian B

Referred material:

	Site	
UB 20861	64.18	left scapula
UB 20862	64.20	right scapula
UB 20863a-c	64.19	skull fragments
UB 20864	?	vertebra fragment
UB 20865a	64.13	rib fragments
UB 20865b	64.17	rib fragments
UB 20865c	64.18	rib fragment (in matrix)
UB 20865d	64.19	rib fragments

UB 20865e	64.20	rib fragment
UB 20865f	64.21	rib fragment
UB 20865g	?	rib fragment (in matrix)
UB 20865h	?	rib fragment (in matrix)
UB 20865i	?	rib fragment

Age and locality: Lower Miocene (Burdigalian) of Gebel Zelten (28°-29° N., 19° 30'-20° 30' E.), Libya.

Remarks: None of this material was associated with remains of either Rytiodus zeltenensis or Metaxytherium sp. indet., and it is too incomplete to be reliably referred to either of these forms. Only the scapulae are worthy of description.

Anatomical description:

Scapulae

Much of the left scapula (20861), including the cranial border, vertebral border , supraspinous fossa, and acromion process, is missing. Most of the thick, rounded caudal border is intact. The spine is broken at both ends, but it was probably a very stout structure when complete; the free edge of the spine is curved over the infraspinous fossa. The glenoid cavity is oval in outline.

The blade of the right scapula (20862) is more complete than that of the left, but the glenoid cavity is missing. The caudal border of the blade is slightly concave, but the shape of the vertebral and cranial borders cannot be determined because they are badly damaged. The spine is blunt and disappears towards the vertebral border. There is no trace of an acromion process, but the shaft is broken at this point.

CHAPTER 2: NEW FOSSIL SIRENIA FROM FRANCE

HISTORICAL BACKGROUND AND GEOLOGY

The various Cenozoic sedimentary basins of France have yielded numerous sirenian remains (including complete skeletons) from Oligocene, Miocene, and Pliocene strata, but Eocene material has been very scanty and incomplete. Up until now the only Eocene sirenians from France have been represented by isolated teeth from several localities in the Aquitaine Basin, which have been referred to *Protosiren* and *Eotheroides* (Sickenberg, 1934; Richard, 1946). The existence of new, undescribed Eocene sirenian material from southern France was brought to my attention in October, 1971 - until then its importance had apparently not been recognized. The initial find of vertebrate material was made in August, 1969 at Taulanne, near Castellane, by members of a geological field party from the Universiteit van Amsterdam. Nobody in this party was acquainted with vertebrate remains so they sent for Dr. M. Freudenthal of the Rijksmuseum van Geologie en Mineralogie, Leiden, and he promptly identified the bones as belonging to sirenians and he wrote an informal description of the find (Freudenthal, 1970). Material was distributed between Amsterdam, Leiden, and the Université de Lyon, but only that in the first two institutions has been studied by the author.

The bones were found in a very hard sandstone that was covered by a reef deposit containing foraminiferans (M. Freudenthal, pers. comm.) - the sandstone lay unconformably on Upper Jurassic limestone. The foraminiferans from above the sirenians have been identified as *Nummulites variolarius* (Lamarck), a wide-ranging Eocene species (Werner, 1970). Since *N. variolarius* is invariably associated with *N. laevigatus* in the lower part of the Lutetian (Middle Eocene), it is most likely that the sirenian-bearing sandstone at Taulanne is upper Lutetian-Priabonian (Middle-Late Eocene) in age. The detailed geology of the Taulanne region is presently being worked on by members of the Geologisch Instituut, Amsterdam.

SYSTEMATIC DESCRIPTION

Order SIRENIA Illiger 1811

(see Chapter 1)

Superfamily PRORASTOMOIDEA superfam. nov.

(see Chapter 1)

Family EOTHEROIDIDAE fam. nov.

Diagnosis: Lacrimal duct and foramen present; alisphenoid canal absent; short superficies meatus; processus fonticulus absent; periotic isolated from rest of braincase. Incisor tusks beginning to enlarge.

Remarks: Contains the genera Eotheroides and Prototherium.

Genus EOTHEROIDES Palmer 1899

Synonymy: Eotherium Owen 1875
Eosiren Andrews 1902
Archaeosiren Abel 1913

Sickenberg (1934) considered Eosiren and Archaeosiren to be synonymous with Eotherium, but Simpson (1932) had already shown that Eotherium Owen 1875 was preoccupied by Eotherium Leidy 1853 and must be replaced by Eotheroides Palmer 1899.

Diagnosis: Skull not dolicocephalic. M^2 larger than M^3. Humerus short and fat.

Type species: Eotheroides aegyptiacum (Owen) 1875; Middle Eocene (Lutetian) of Gebel Mokattam, Egypt.

Included species: E. libycum (Andrews) 1902
E. stromeri (Abel) 1913
E. abeli (Sickenberg) 1934

Distribution: Middle-Upper Eocene of France and Egypt.

Remarks: This is the only Eocene sirenian genus that occurs in deposits on two different continents.

Eotheroides cf. E. aegyptiacum (Owen) 1875

Referred material:	GIA Hs 69-3	left mandibular ramus
	GIA Hs 69-4	right mandibular ramus
	GIA Hs 69-5	braincase
	GIA Hs 71-19	skull
	GIA Sm 71-101	skull and mandible
	GIA Sm 71-102	isolated right M^3
	RGM St. 177774	skull
	RGM St. 177775	skull

Age and locality: Middle-Upper Eocene (Lutetian-Priabonian) of Taulanne, France

Remarks: These new sirenian remains from the north shore of Tethys constitute the first unequivocal trans-Tethyan correlation with the well-known Eocene sirenian faunas of nothern Africa. If, as seems likely, more material is retrieved from this site, it will provide the basis for the type of population study that has previously been impossible with sirenians.

Anatomical description:

The genus Eotheroides has been well documented in the literature (Andrews, 1906; Abel, 1913; Sickenberg, 1934), so it would be tedious to give a detailed description of the new material now available. The following account will be restricted to a comparison of the Taulanne material with other species of Eotheroides, and to features that have received little attention from the earlier authors. Only one of the Taulanne specimens (the mandible belonging to Sm 71-101) is complete, but by utilizing features from different specimens it is possible to construct an overall picture of the morphology of the rest of the skull.

Skull:

The most complete skull (Hs 71-19) has an overall shape that is closer to that of Eotheroides aegyptiacum and E. libycum than it is to that of E. stromeri. The Taulanne sirenian, E. aegyptiacum, and E. libycum have relatively slender skulls whereas E. stromeri has a much more robust skull; the differences are most distinct in the fronto-parietal region (Sickenberg, 1934, p. 195).

The premaxillae are very complete on Hs 71-19 and are comparable with those illustrated by Andrews (1906, pl. XX) and Sickenberg (1934, pl. II) for E. libycum. Unfortunately the premaxillary region of E. aegyptiacum has not been illustrated by these authors, but there is no reason to think that it was dissimilar to that of E. libycum. The premaxillary rami of Hs 71-19 are inserted posteriorly between the nasals and the frontals, and are contained in depressions along the anterolateral edge of the nasals. The maxillae are remarkable for their considerable palatal width, which was a feature used by Sickenberg (ibid., p.196) to differentiate E. aegyptiacum from E. libycum.

The nasals of the Taulanne specimens meet in the mid-line anteriorly, but are separated for a short distance posteriorly by a forward extension of the frontals (St. 177775). This arrangement produces a W-shaped suture between the nasals and the frontals as is also shown by the example of E. aegyptiacum illustrated by Abel (1913, pl. I). The nasals are also very convex.

The left lacrimal of St. 177775 is the best preserved and it takes part in the formation of the orbital border as does the corresponding bone in E. aegyptiacum (Abel, 1913). Reinhart (1959) described a broken skull of Eotheroides sp. indet., in which the lacrimal did not form part of the orbital border and contacted the dorsal edge of the jugal. In E. aegyptiacum the lacrimal is separated from the jugal by the maxilla, but the situation in St. 177775 cannot be resolved because the jugal is missing. There is a characteristic large duct present in the left lacrimal of St. 177775.

The frontals of the French specimens are characteristic of Eotheroides because they form the medial walls of the orbits (St. 177774), whereas in Protosiren this function is performed by the ethmoid. The parietals bear pronounced temporal crests and have a V-shaped suture with the frontals. The sagittal length of the parietals is somewhat less than that of the frontals - a feature that is found in E. aegyptiacum rather than E. stromeri. The occipital region is very badly preserved on all the Taulanne specimens and does not show any distinctive characters. The basioccipital of St. 177774 has not fused to the basisphenoid. The jugal is a slender bone that has a ventral

extension in Hs 71-19.

The palatines are well preserved on Hs 71-19 and they separate the maxillae in the mid-line as far as the anterior edge of the last deciduous premolar. The sphenoid complex is only adequately preserved on Hs 69-5, where the optic foramen and the sphenorbital canal are intact on each side. The optic foramen is situated dorsal to the sphenorbital canal, and the dorsal wall of the latter bears a slight longitudinal ridge that probably represents the last remnants of the lamina that separated two of its component canals. The pterygoid processes are typical of Eotheroides, being slender and with no indication of an alisphenoid canal. The zygomatic process of the squamosal is slender (St. 177774) as in E. aegyptiacum and bears prominent postglenoid and post-tympanic processes.

The petrotympanic is not well enough prepared on any specimen to show diagnostic features, but there is a short superficies meatus as in all other species of Eotheroides. The cranial cavity of Hs 71-19 bears a sagittal ossified falx cerebri and a transverse ossified tentorium cerebelli on its dorsal surface, but these are not prominent.

Mandible:

The mandible belonging to Sm 71-101 is probably the most perfect of any Eocene sirenian because it is complete except for the absence of the right condyle. Although the two halves of the mandible are crushed together, there is no significant deformation of the rami themselves. Very few mandibles of Eotheroides have been illustrated in the past - Abel (1913, fig. 5) showed a reconstruction of the mandible of E. aegyptiacum, and Andrews (1906, pl. XX, fig. 2) and Sickenberg (1934, fig. 19) have both illustrated mandibles of E. libycum. Unfortunately the mandible shown by Abel is formed from the anterior part of an E. aegyptiacum mandible and the posterior part of an E. abeli mandible (Sickenberg, 1934). Thus the Taulanne mandible must of necessity be compared with that of E. libycum since not enough is known about the mandible of E. aegyptiacum.

The differences between the two mandibles are slight and are not useful for identifying species. The anterior edge of the vertical ramus of Sm 71-101

is inclined anteriorly as far as the back of M_3, but in E. libycum it is vertical (Sickenberg, 1934, fig. 19). There is a distinct projection about half-way up the posterior edge of the vertical ramus of Sm 71-101 that is also present in E. libycum, E. abeli, and Prototherium veronense - the dorsal margin of this projection is on a level with the alveolar margin. The ventral curvature of the horizontal ramus is the same as in E. libycum. The internal surface of the mandibular angle bears a distinct shelf that is especially prominent on the two broken pieces of mandible (Hs 69-3, Hs 69-4) - this shelf is also present, but to a lesser degree, in Dugong. The shelf forms the ventral of the fossa for the internal pterygoid muscle. Another depression occurs on the internal surface of the mandible below the mandibular condyle, marking the area of attachment of the external pterygoid muscle.

Dentition:

The most important feature of the Taulanne material is the excellent preservation of the dentitions of some of the specimens. Unfortunately only one specimen (Hs 71-19) has an intact rostrum, so very little of the premaxillary dentition is conserved. However, the post-canine dentition of the upper jaw is well represented by intact molars and the alveoli of the premolars. The mandibular dentition is best preserved on Sm 71-101.

Dentition of the premaxillae and maxillae:

The only premaxillary teeth of which we have any evidence are the two enlarged first incisors of Hs 71-19. These teeth are represented only by the remains of their alveoli, which indicate that the first pair of incisors was becoming tusk-like. The two other pairs of upper incisors cannot be traced because the alveolar margins of the premaxillae are badly broken, but there is evidence for them on other species of Eotheroides. The canines are most probably denoted by a pair of isolated alveoli on Hs 71-19 and St. 177775.

The maxillary dentition is present on four specimens (St. 177774, St. 177775, Sm 71-101, and Hs 71-19), which can be arranged according to age (see Table 9). Apart from an erupting tooth on St. 177774 the premolars are only represented by their empty alveoli. There were apparently four permanent premolars - the last of which is late in erupting because dP^4 is retained until

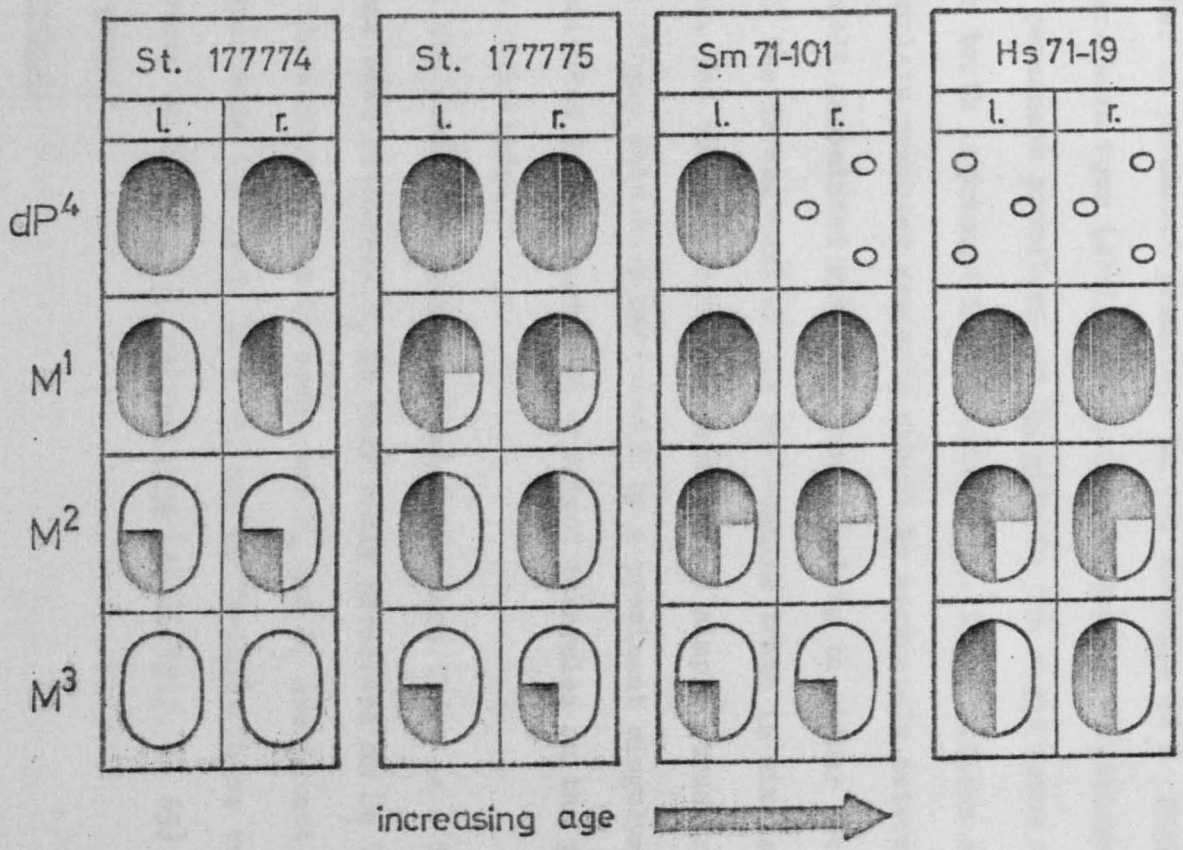
after M^3 has come into use. A total of three premolar alveoli are visible in front of the molariform dP^4 of Hs71-19, but there is no certainty as to the number of premolars that they represent. Four premolar alveoli are found in most other species of the genus and it has been assumed previously that all the premolars of Eotheroides were single-rooted. In three of the Taulanne specimens (St. 177775, Hs 71-19, and Sm 71-101) the two alveoli immediately in front of dP^4 are very close together, but the third alveolus is separated from them by a prominent diastema - the premolar alveoli of E. libycum are equally spaced at c.13mm intervals (Andrews, 1906). If the previous authors were correct in their assumptions that all of the premolars had a single root then these three alveoli should be assigned to P^1, P^2, and P^3 - P^4 having not yet erupted. Nevertheless, more complete premolar sequences must be found before a conclusion can be reached as to the number of permanent premolars and their roots.

The last deciduous premolar is present in three individuals, but it is worn flat in even the youngest one (St. 177774). It is retained in the maxilla at least until M^3 is beginning to show wear, but it is lost with increasing age (see Table 9). Where dP^4 is missing it is seen to have had three roots - one internal and two external.

The full complement of upper molars is found on three Taulanne individuals (St. 177774, St. 177775, and Sm 71-101), and due to differences in age of the three specimens the teeth show great variation in the degree and pattern of crown wear. M^1 and M^2 are consistent with the same teeth of Eotheroides species (Abel, 1913; Sickenberg, 1934), but M^3 shows conspicuous differences in morphology that illustrate the wide range of variation within the species. The characteristic form of the M^3 of Eotheroides is exhibited by St. 177775 and Hs 71-19, but an aberrant type of tooth is present on both sides of Sm 71-101. Each of these latter teeth is unusual because of the complete absence of the hypoconule and its associated cuspules, which are found behind the metaloph in a normal Eotheroides M^3. The absence of this group of cuspules results in a marked concavity on the posterolabial surface

TABLE 9

Four stages of tooth wear in Eotheroides cf E. aegyptiacum



KEY

- empty alveolus
- crown worn flat
- lophs wearing flat
- cusps coalescing to form lophs
- individual cusps showing wear
- crown unworn (including unerupted teeth)

of each molar. This part of the tooth was also missing from a tooth examined by Sickenberg (1934, p. 142) (see below). Other, less important, differences are apparent, but they are not so significant.

Dentition of the mandible:

The mandibular dentition is even more difficult to interpret than that of the premaxillae and maxillae. The anteroventrally inclined symphysial surface of the mandible belonging to Sm 71-101 bears four pairs of very shallow alveoli, which are the only evidence for the existence of incisors and canines in the lower jaw. The shallowness of the alveoli is due to them being infilled with cancellous bone, and this shows that even at this early stage of sirenian evolution the anterior teeth were markedly reduced.

The number of permanent premolars in the mandible of E. aegyptiacum is thought to have been four (Abel, 1913), but the number of deciduous teeth is unknown. Two permanent premolars are in situ in the right ramus of Sm 71-101, and another tooth is present in the left ramus. The positions of these teeth in the complete premolar sequence cannot be accurately determined because the alveoli associated with them could belong to either deciduous or permanent teeth. The arrangement of the post-canine teeth is similar to that in the upper jaw. The three intact premolars have a simple structure consisting of a single main cusp surrounded by a prominent cingulum. This cingulum is subdivided into a number of distinct tubercles on the posterior premolar of the right side.

Between the permanent premolars and the molars there is a deciduous premolar that has been retained. M_1 is very badly preserved on Sm 71-101 and very little of its structure can be seen, but M_2 and M_3 are intact though worn on three specimens (Hs 69-3, Hs 69-4, and Sm 71-101). These teeth have a similar structure to those of E. aegyptiacum (Abel, 1913, p. 69) and other members of the genus.

Tooth eruption:

The method and sequence of tooth eruption in Eocene sirenians is of interest because of the unusual modifications this process exhibits in later

genera. It has been impossible to study eruption on Eocene species before due to the scarcity of good material, but this small sample from Taulanne increases our knowledge in this field. When more material becomes available there should be an almost complete record of the sequence of tooth replacement in Eotheroides.

As mentioned above, the four specimens with good maxillary dentitions can be grouped according to relative age (see Table 9). This is possible by comparing the amount of wear on the corresponding teeth of the different specimens. The youngest individual (St. 177774) is characterized by having only a partly erupted M^3 - M^2 and M^1 of this specimen show progressively advanced wear stages and dP^4 is worn flat. Although this last tooth has lost all traces of its lophodont structure it is still retained in the maxilla, thus effectively increasing the length of the upper cheek tooth row. The occurrence of four molariform cheek teeth for a short period in the animal's life is common to Eotheroides spp. and Prototherium veronense (Abel, 1913; Sickenberg, 1934). The molariform dP^4 of Hs 71-19 is not lost until the M^3 is in full use.

Anterior to dP^4 on St. 177774 there is an erupting tooth that should be P^4, but the little of it that is visible does not correspond very closely with the previous descriptions of this teeth. The erupting tooth on St. 177774 is elongated and bears four pointed cusps, three of which are aligned longitudinally and increase in size posteriorly with the fourth situated lingual to the largest of these. This tooth most closely resembles the P^4 of E. aegyptiacum (=E. abeli of Sickenberg) described by Abel (1913). However, the latter tooth is said to be basically tricuspid and Abel does not provide an illustration to show its structure. The P^4 of E. libycum was illustrated by Andrews (1906, fig. 2), who described it as being a single cone (Andrews, 1902). If Andrews and Abel were correct in their identifications of P^4 it suggests that the last premolar of Eotheroides was reduced from three cusps to one cusp between the Middle and Late Eocene. Although the tooth on the Taulanne specimen has four cusps it may represent an even earlier stage in the evolution of the P^4 of Eotheroides, but because the most posterior cusp

is the largest there is a chance that it is a deciduous tooth (dP^3?) rather than a permanent one. The lack of information on the upper premolars of Eotheroides may hopefully be remedied by more material from Taulanne, but until this material is available we cannot reach any definite conclusions as to the morphology and the arrangement of these teeth.

Since only one mandible is known from Taulanne it is impossible to deduce the mode of tooth replacement. However, in Sm 71-101 the individual cusps of M^3 have begun to coalesce and a deciduous premolar is still in place in the right ramus. The mandibular dentition is therefore similar to the maxillary one in this respect. The reduction (or loss ?) of the mandibular incisors and canines is an early example of a feature that is to be prominent in all later sirenians.

REVISION OF CERTAIN EOCENE SIRENIAN SPECIMENS

The existence of Eotheroides cf. E. aegyptiacum in the northern parts of Tethys during the Eocene demands a re-examination of some of the previously described Eocene sirenian material from this area.

Eotheroides and Protosiren from the Aquitaine Basin

Richard (1946), in her comprehensive survey of the fossil mammals of the Aquitaine Basin, listed three sites near the mouth of the Gironde that have yielded remains of Eotherium (=Eotheroides). She recorded rib fragments from Blaye (Lutetian), a molar from Villeneuve (Bartonian), and a specimen that has since been lost from Moulin de Calon (Ludian = upper Bartonian). Only the molar can be said to be reliably identifiable.

Sickenberg (1934) described three molars from the Calcaire de Blaye of the Aquitaine Basin that he referred to a new species of Protosiren, P. (?) dubia. Prototherium veronense was known from the Late Eocene of Monte Zuello, Italy, at this time, but Sickenberg thought that the French teeth were too

small for this genus. He listed the teeth as a right M^3, a right M_2, and a left M^2; because the M^2 and M^3 differed in size only slightly he referred all three teeth to Protosiren. The absence of any associated skull material makes this identification very dubious, and the two upper molars (Sickenberg, 1934, fig. 36) do not appear to possess any characters that can be used to separate M^2 and M^3 - in fact the M^3 illustrated by Sickenberg is an almost exact mirror image of the M^2. If each of these teeth is considered as an M^2 it would eliminate the size feature that Sickenberg used as a Protosiren characteristic, and, seen thus, these teeth are indistinguishable from those of Eotheroides cf. E. aegyptiacum.

Sickenberg (1934) also described a skull fragment as belonging to Protosiren sp., but there is no evidence that it could not equally well have belonged to a species of Eotheroides.

There is therefore no evidence for more than one genus of sirenian occurring in the Eocene strata of southern France.

Eotherium (=Eotheroides) spec. I

In his study of the genus Eotherium (=Eotheroides), Sickenberg (1934) was left with two specimens that could not be satisfactorily referred to any of the recognized species. Both specimens came from the Upper Mokattam Series (Upper Eocene) and were labelled by Sickenberg as Eotherium spec. I and Eotherium spec. II. Eotherium spec. I is a left maxillary fragment containing M^2 and M^3 that only differs from the typical E. libycum because of its smaller size and the primitive structure of the M^3. The so-called primitive features of this tooth include the large size of the protocone, the weakly developed metaloph, the insignificant metacone, and the absence of the hypocomule and associated cuspules. The two M^3's belonging to one of the Taulanne skulls (Sm 71-101) have essentially the same structure as the above tooth, although the rest of the specimen is identical with the other material from that site. Since all of the Taulanne material can be referred to a single

species, the absence of the posterior group of cuspules from M^3 is taken to represent the wide range of intraspecific variation (in this case in Eotheroides cf. E. aegyptiacum).

Reviewing Eotherium spec. I in the light of this new evidence indicates that it is most probably a morphological variant of Eotheroides libycum.

Eotherium (=Eotheroides) majus Zdansky

This species was erected by Zdansky (1938) to accommodate an isolated M^2 from the Lower Mokattam Series (=Mokattam Formation) of Egypt. According to Zdansky, the only differences between this tooth and the M^2 of Eotheroides illustrated by Abel (1913, pl. II) are a slight variation in shape and a greater size for the former. These features are notoriously variable in sirenian teeth (cf. Taulanne specimens) and should not be used as specific characters on their own. It is not possible to compare the measurements of the M^2 of E. majus with those of the M^2 of E. aegyptiacum because the tooth dimensions of the latter species have not been given in the literature and the best specimens are now inaccessible. The tooth of E. majus, however, is larger than any of the M^2's from Taulanne. It is very worn and the cusps of the two lophs have coalesced, obscuring any diagnostic features that the crown may have had. The specimen is best referred to Eotheroides sp. indet. rather than being used as the basis for a new species.

CHAPTER 3: NEW FOSSIL SIRENIA FROM ARGENTINA

HISTORICAL BACKGROUND

Fossil sirenians have been described from the Neogene of Argentina by Ameghino (1883), and Pascual (1953; 1966). These two authors were principally concerned with fossil trichechids, and they described the first pre-Pleistocene members of this family.

In February, 1898, the British Museum (Natural History) purchased an incomplete sirenian mandible from the Rev. Dr. Spilsbury. This specimen is listed in the museum's records as coming from Parana, Argentina, and being ?Pliocene in age; although having never been described it has up until now been referred to the genus Manatus (=Trichechus). New material that has been found since this specimen was originally identified necessitates a reappraisal of its position within the Trichechidae and of its importance to sirenian evolution.

SYSTEMATIC DESCRIPTION

Superfamily TRICHECHOIDEA superfam. nov.

Diagnosis: Rostrum small and little deflected. Numerically increased dentition; incisor tusks absent; cheek teeth continuously replaced from rear. No bicipital groove on humerus; carpals little fused; hind limbs reduced and functionless; ilium greatly reduced or absent; ischium relatively large and triangular. Six cervical vertebrae; usually seventeen thoracic vertebrae.

Remarks: This superfamily contains only one family, the Trichechidae.

Family TRICHECHIDAE Gill 1872

Diagnosis: As for superfamily.

Remarks: This sirenian family is very poorly represented in the fossil record, but its history goes back at least as far as that of the Dugongidae.

Genus RIBODON Ameghino 1883

Diagnosis: Maximum of four cheek teeth present in mandible at any one time; cheek teeth are bilophodont with prominent hypoconulid.

Type species: Ribodon limbatus Ameghino 1883; Mio-Pliocene (Mesopotamian) of Parana, Argentina.

Distribution: Mio-Pliocene of Argentina and Colombia.

Remarks: So far this genus is only known from cheek teeth and fragmentary mandibles.

Ribodon limbatus Ameghino 1883

Diagnosis: As for genus.

Referred material: BM(NH) M7073 left mandibular ramus with two cheek teeth

Age and locality: ?Pliocene of Parana, Argentina.

Anatomical description (Plates 28 and 29):

The specimen is an incomplete left mandibular ramus lacking the symphysial region and part of the ascending ramus, but containing two complete cheek teeth and the remains of two others.

The horizontal ramus is larger than that of Trichechus, and it is broken anteriorly just behind the mandibular symphysis. The external surface of the ramus is pierced by six small foramina, at least two of which communicate with the mandibular canal. This canal opens internally below the posterior end of the functional tooth row, and the mandibular foramen is traversed by a narrow bridge of bone. The internal surface of the ramus is expanded mediad at the symphysial end to accommodate the lingual musculature, but this region is very incomplete. The thin bone of the dental capsule is unfortunately missing, but the cavity that housed the capsule is present and is much larger than that of Trichechus.

The ascending ramus is only partially present and lacks most of the coronoid process, the mandibular condyle, and the mandibular angle. The anterior border of the ascending ramus is almost vertical, unlike the anterodorsally

PLATE 28

Ribodon limbatus

M7073: lateral view of left mandibular ramus

PLATE 29

Ribodon limbatus

M7073 : medial view of left mandibular ramus

FIGURE 40

A : Drawing of Plate 28

B : Drawing of Plate 29

PLATE 28

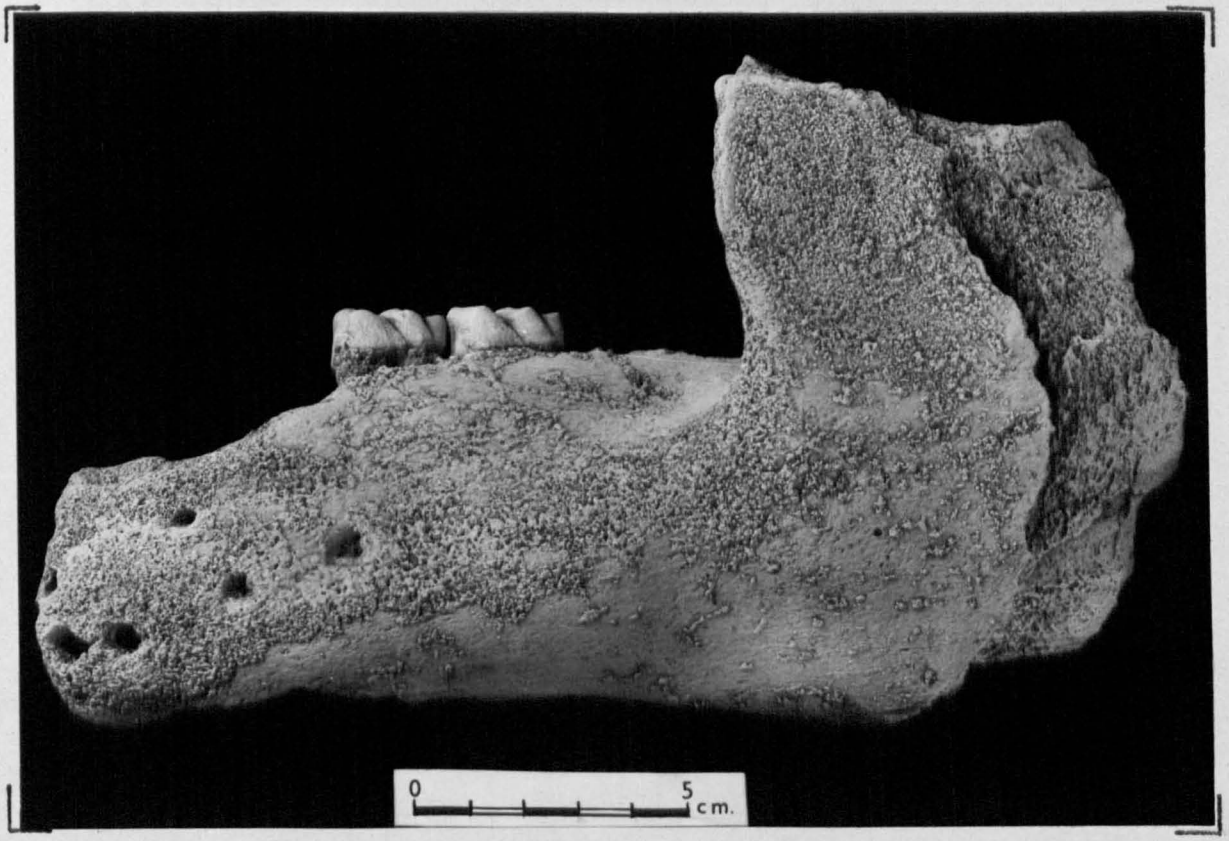


PLATE 29

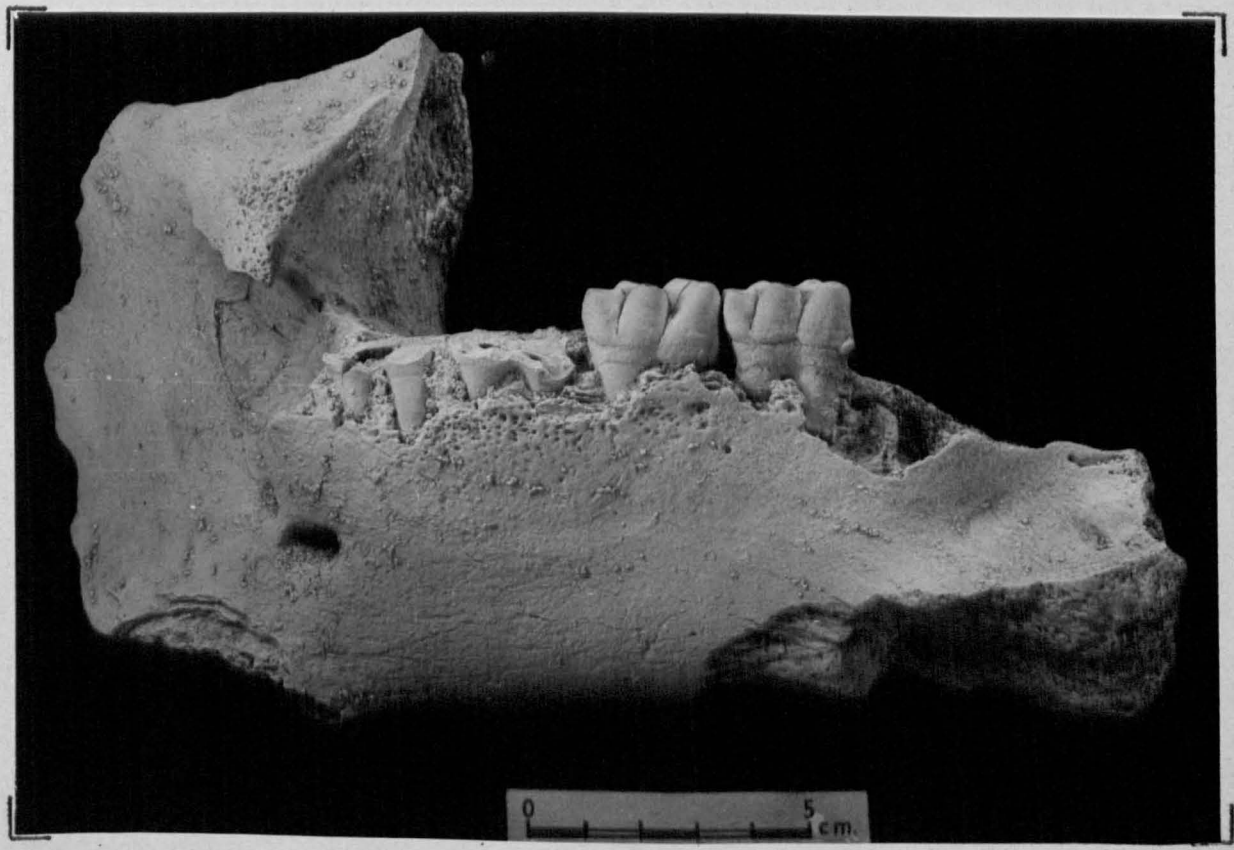
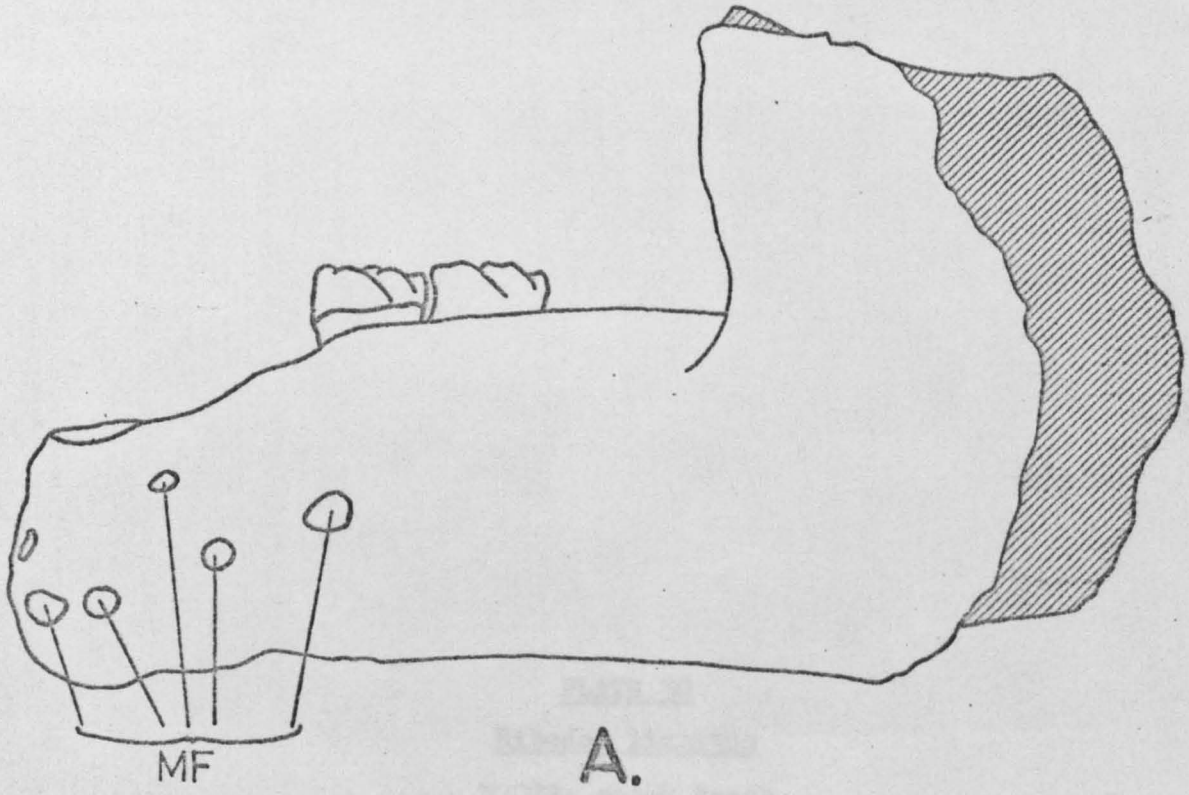
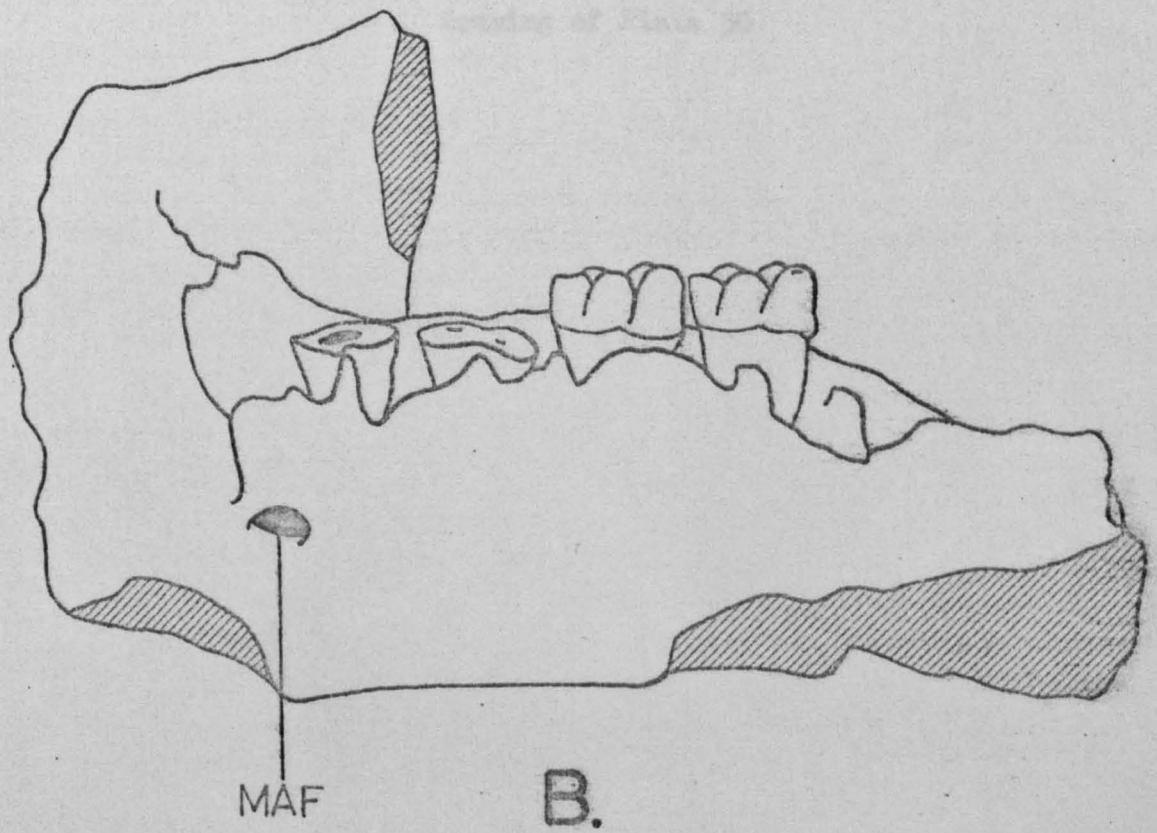


FIG. 40



A.



B.

PLATE 30

Ribodon limbatus

M7073: cheek teeth

FIGURE 41

Drawing of Plate 30

PLATE 30

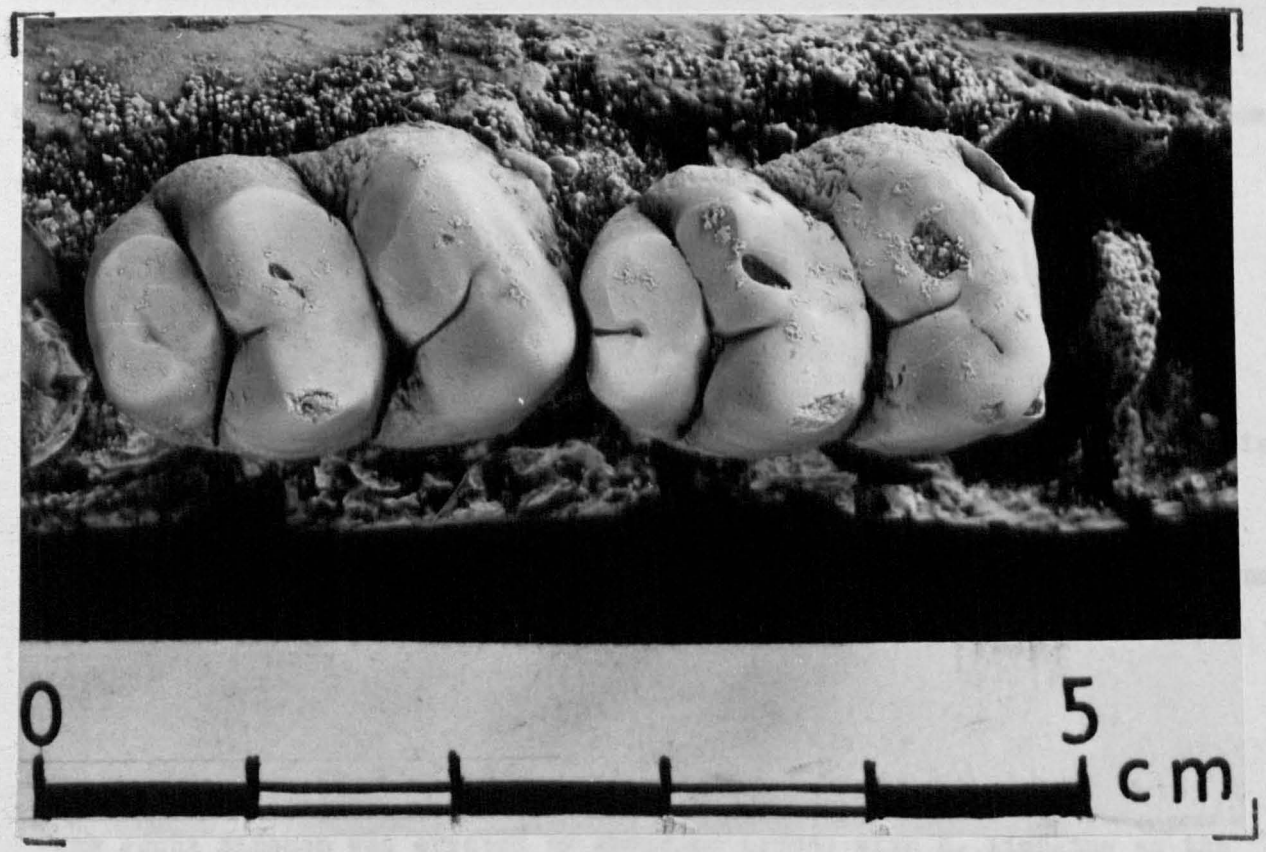
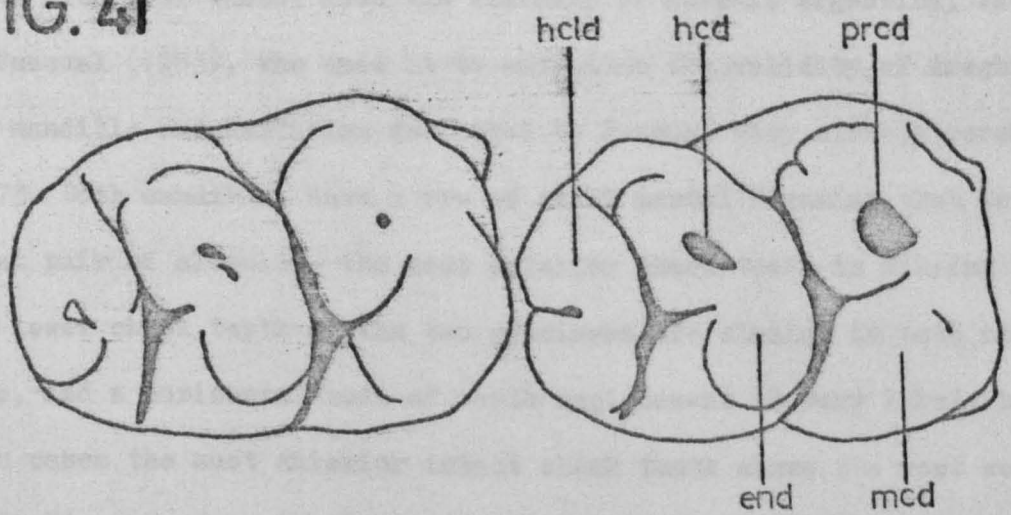


FIG. 41



inclined anterior border of the ramus of Trichechus.

The dorsal surface of the horizontal ramus is relatively complete, so that it is possible to study the dentition. The most anterior pair of alveoli is empty, but certainly contained a single tooth that had two transverse roots. The next two pairs of alveoli contain two intact cheek teeth that differ from those of Trichechus (see Plate 30); two more teeth are represented by just their roots. The intact teeth are basically bilophodont with a large hypoconulid. Each loph is composed of two cusps (the lingual cusp being the higher and more anterior in both cases), and the lophs are separated by a transverse valley. Behind the metalophid there is a large hypoconulid that is lower and flatter than either of the two lophs, and which is separated from the metalophid by a very shallow groove. There appears to have been a maximum of four cheek teeth in occlusion at any one time.

Comparison and discussion:

The genus Ribodon was erected by Ameghino (1883) with R. limbatus as the type species. Ameghino recognized the sirenian affinities of the isolated cheek teeth which he found in the "Piso mesopotámico de la formación patagónica" of Argentina, and he placed the new genus in the Halitheridae. Simpson (1932), however, did not include Ribodon in his revised classification of the Sirenia. More complete material, including a broken left mandibular ramus with four teeth, from the vicinity of Parana, Argentina, was described by Pascual (1953), who used it to establish the validity of Ameghino's genus. The mandible and dentition described by Pascual very closely resembles that of M7073. Both mandibles have a row of small mental foramina that ends below the first pair of alveoli - the most anterior cheek tooth is missing in both cases. The lower cheek teeth of the two specimens are similar in both morphology and size, and a horizontal mode of tooth replacement is very likely because in both cases the most anterior intact cheek tooth shows the most wear and in M7073 it appears to be encroaching upon the empty alveolus in front of it. Pascual (1953) claimed that Ribodon was distinct from Trichechus because of its shorter functional tooth row (four teeth instead of the five to seven of

Trichechus) and because the structure of its teeth is more primitive.

Pascual (1953) suggested that Potamosiren magdalenensis Reinhart, a Late Miocene trichechid from Colombia that was described by Reinhart (1951), was the same as Ribodon. The only known cheek tooth of Potamosiren is larger than, but structurally very similar to, the teeth of both Pascual's specimen and M7073. The only significant difference that Pascual noticed between Ribodon and Potamosiren was in the structure of the mandible, but he attributed this to the broken nature and advanced age of that of the latter. Reinhart (1951) assumed that both of the specimens (isolated tooth and broken mandible) he referred to Potamosiren came from the same individual because of their close proximity when found. However, the mandible resembles that of a trichechid only because of its slender form and its anteriorly-directed coronoid process. The most plausible explanation of this mandible is that it belongs to a member of the genus Metaxytherium; the presence of alveoli for only three cheek teeth and the shape of the coronoid process are two features shared by the mandibles of Metaxytherium and Potamosiren. Kellogg (1966) has described part of a left maxilla from the Upper Miocene of Colombia that he assigned to a new species of dugongid, Metaxytherium ortegense; this specimen was found to the north of the Potamosiren locality and is probably from the same stratigraphic unit. The presence of only three (and maybe even only two) functional cheek teeth in the mandible of Potamosiren is a dugongid rather than a trichechid character, and the fact that the dental capsule of Potamosiren is infilled with cancellous bone suggests that it had a finite number of teeth rather than the continuous sequence found in Trichechus and apparently also in Ribodon. The reputed trichechid sirenian Potamosiren magdalenensis Reinhart is therefore a chimera - the isolated tooth does belong to a trichechid, but to the previously described genus Ribodon, whereas the mandible is referable to a dugongid, most probably Metaxytherium.

CHAPTER 4: A REVIEW OF THE SIRENIA

THE ROSTRUM AND TUSKS OF THE DUGONGIDAE

The prominent, deflected premaxillary region present in most genera of the family Dugongidae has not been satisfactorily explained in the previous literature on the group. This feature, which is found in no other mammal group, is well developed in the earliest members of the family, and its presence is heralded in the Protosirenidae and Eotheroididae. This extreme modification of the premaxillae is accompanied by a reduction of both the premaxillary and maxillary dentitions, a character well illustrated by Dugong itself. The drastic change in the shape of the anterior part of the skull has also had a marked effect on the structure of the mandible, which becomes truncated anteriorly with the symphysial region facing anterodorsally. The restriction of these modifications to the front of both jaws suggests that they are associated with either defensive or nutritional requirements. Since sirenians are primarily inhabitants of rivers and shallow coastal areas, they are unlikely to be preyed upon by terrestrial or aquatic predators - so the latter function would be more likely.

Very little research has been carried out on the food preferences or feeding habits of Dugong, but various authors have listed the plants that it is said to eat (Prater, 1929; Sculthorpe, 1967; Bertram & Bertram, 1968; Kingdon, 1971). The food plants of the dugong belong to various families of aquatic monocotyledons, and the distribution of the dugong is controlled by the availability of large areas of these plants. Although these "dugong grasses" have extensive leaf systems, it is believed that the dugong has a preference for the roots. The "grasses" possess lily-like rhizomes that are anchored into the soft sediment of sandbanks by an adventitious root system. It is believed by the natives of Australia, who hunt the dugong, that the animal only consumes the rhizomes, and the hunters can then locate their prey by the resultant floating mass of "grass" (Troughton, 1941). Kingdon (1971) has also noted that the dugong finds the rhizomes edible, and that it

is possible to follow the trails of disturbed substrate left by the feeding animals. He remarked that the dugong is only capable of feeding off of the substrate and cannot eat floating vegetation. This method of feeding is relatively easy for a terrestrial herbivore, but the adaptations associated with an aquatic way of life present problems.

Sirenians and cetaceans are remarkable because of their very compressed cervical vertebrae, and consequently very short necks. Although this feature is necessary for streamlining the body, it also imparts a great deal of immobility to the head. In order to dig for roots etc. it is imperative to be able to lower the head to ground level or to develop a structure that reaches the ground without the head being appreciably lowered. Terrestrial mammals have adopted the former method (the elephant being a notable exception), but the dugongids have had to modify the skull in order to feed whilst keeping the body as close to the horizontal as possible. They have achieved this by developing the deflected premaxillae as a ventral extension to the anterior part of the skull.

The rostrum consists basically of a pair of enlarged upper incisors that are surrounded by the adjacent parts of the premaxillae. Some Eocene sirenian genera have already begun to show signs of enlarged incisors, but, although there is a slight deflection of the premaxillae in these forms, the rostrum does not become prominent until the Oligocene. The ventral elongation of the premaxillae was presumably necessary to protect and strengthen the elongated incisors as they were dragged through the substrate. The walrus, Odobenus rosmarus (Linnaeus), has enlarged canines that are strengthened by being firmly rooted in the maxillae and having a robust shape. The walls of the canine alveoli in Odobenus extend ventrally to secure the teeth. The upper incisors of Dugong grow from persistent pulps and have unusual anterolateral wear facets that are probably caused by the continual movement of the large upper lip (Fernand, 1953) rather than by the abrasive action of unconsolidated sediment (Troughton, 1941). The incisors of the adult male dugong erupt on either side of the "upper jaw pad", but they remain buried in the immature

males and adult females - there is no difference between the unerupted teeth of males and females. This case of sexual dimorphism in living dugongids brings us to the issue of tusklessness in certain of their fossil relatives.

Qualitative sexual dimorphic characters are usually limited to ungulates in the Mammalia, and are best represented by horns and antlers (Kurtén, in Westermann, 1969). Qualitative dimorphism of the dental series is relatively rare, but it has been noted in Equus and some proboscideans. No work has been done on sexual dimorphism in fossil sirenians even though both tusked and tuskless species have been described.

Five species of tuskless dugongids, excluding Hydrodamalis gigas, have been reported in the literature:

Thalattosiren petersi (Abel) 1904	Middle Miocene
Hesperosiren crataegensis Simpson 1932	Middle Miocene
Caribosiren turneri Reinhart 1959	Middle Oligocene
Halianassa vanderhoofi Reinhart 1959	Upper Miocene
Metaxytherium calvertense Kellogg 1966	Middle Miocene

These species retain their cheek teeth and, apart from the absence of the enlarged incisors, they all closely resemble previously described tusked species. The absence of incisor tusks has been taken to be a taxonomic character in the past because both sexes of Dugong possess them. The tusks of the female dugong are noticeably smaller than those of the male and do not penetrate the gums because they are resorbed at their bases. The great similarity between the cranial anatomy of the five tuskless species and that of certain species with tusks is indicative of a sexual variation rather than a taxonomic one.

Thalattosiren petersi is a tuskless sirenian that combines some of the characters of both Halitherium and Metaxytherium - its nasals join in the mid-line like those of Halitherium, but it has the same cheek tooth formula as Metaxytherium. T. petersi is younger than any species of Halitherium and is presumably a late remnant of the Halitheriinae that paralleled the Metaxytheriinae in tooth reduction. It is best retained in a distinct genus

because of its transitional characters.

Simpson (1932) described Hesperosiren crataegensis on the basis of a crushed skull and various post-cranial remains from the Middle Miocene of Florida. Since the skull was badly deformed, Simpson had a model prepared to represent its presumed original appearance. He at once noted the absence of incisors and realized that his material was distinct from that of the other known tuskless genera, Hydrodamalis and Thalattosiren. Simpson also remarked on the close resemblances between Hesperosiren and the Metaxytherium-Felsinotherium complex, although he thought that the absence of incisors and the shape of the rostrum necessitated the erection of a new genus. However, he placed the new taxon in the subfamily Halitheriinae together with Halitherium, Metaxytherium, and Felsinotherium.

In his review of the Sirenia, Reinhart (1959) described two new tuskless forms from the New World; the Oligocene Caribosiren turneri, which has been discussed above in relation to Rytiodus zeltenensis (see Chapter 1), and the Miocene Halianassa (=Metaxytherium) vanderhoofi. Domning (1970a) considered H. vanderhoofi to be a junior synonym of Metaxytherium jordani Kellogg 1925, a tusked sirenian from the Upper Miocene. This occurrence of a true Metaxytherium without tusks was the first piece of evidence for sexual dimorphism in the Neogene Dugongidae, and it was substantiated by the finding of another tuskless dugongid, Metaxytherium calvertense, in the Middle Miocene rocks of Maryland (Kellogg, 1966). Since M. jordani (=H. vanderhoofi) is from California, tuskless sirenians are now known from both sides of the United States.

The theory of sexual dimorphism in sirenians could not be supported when Thalattosiren and Hesperosiren were described, but this new material can be used in a re-examination of the theory. Although Thalattosiren petersi has certain characters that warrant placing it in a genus of its own (see above), the absence of incisor tusks on the type (and only) specimen is most probably a sexual feature. Similarly, a comparison of the illustrations of Hesperosiren crataegensis (Simpson, 1932, figs 2 & 3) and Halianassa vanderhoofi (=

Metaxytherium jordani) (Reinhart, 1959, figs 4 & 5) shows that the two forms were very similar in overall skull morphology, and a close scrutiny of Simpson's description reveals that his genus is almost indistinguishable from H. vanderhoofi. The characters that Simpson believed to be diagnostic for Hesperosiren are reviewed in the next paragraph and are compared with those of H. vanderhoofi.

Hesperosiren has two small pits at the anterior end of the premaxillae, but there are no incisor tusks; H. vanderhoofi also lacks incisors. Both species have only a slightly deflected rostrum, although Simpson's reconstruction apparently exaggerates the straightness of the rostrum of Hesperosiren. The rostrum is swollen anterior to the mesorostral fossa in both forms, and the posterior rami of the premaxillae are clasped by the frontals. Simpson compared Hesperosiren with Metaxytherium cuvieri (=M. medium) and noted that the mesorostral fossa of the former was relatively longer; in contrast, H. vanderhoofi has a longer fossa than Hesperosiren. The nasals agree in shape and size in both Hesperosiren and H. vanderhoofi, and the temporal crests of both have a similar configuration. Hesperosiren and Metaxytherium (including H. vanderhoofi) both appear to have had nine thoracic vertebrae with demi-facets. The remainder of the characters of Hesperosiren can be safely taken as being characteristic of Metaxytherium, and it was precisely these features that enabled Simpson to place Hesperosiren in the same subfamily as Metaxytherium. No tusked dugongids are known from the Miocene of Florida, but Pliocene forms have been discovered there and specimens probably referable to Metaxytherium occur in South Carolina.

If the presence or absence of tusks is taken to be a sexual character, then Hesperosiren is indistinguishable from members of the genus Metaxytherium, especially M. jordani (including Halianassa vanderhoofi). Without examining the actual specimens it is impossible to say whether Hesperosiren crataegensis represents a new species of Metaxytherium or is merely a female of a previously described species. For the present it is better to allocate it to the genus Metaxytherium as a new species, M. crataegensis (Simpson).

The presumed absence of enlarged incisor tusks in certain female sirenians is most probably due to reduction rather than non-development. All tuskless dugongids have a deflected rostrum (not bent to the same degree in all species) that is intimately associated with the presence of enlarged tusks. It is extremely unlikely that a deflected rostrum could have developed without being stimulated by the growth of enlarged incisors. Metaxytherium crataegensis may have had small, rudimentary incisors in the two small pits on its premaxillae that appear to be the remains of alveoli. These small incisors could have been lost during fossilization. Since many sirenian species are represented by inadequate material, it is possible that sexual dimorphism was much more common than has been previously supposed.

If this suggested sexual dimorphism is to be satisfactorily explained it is necessary to put forward a reason for the retention of tusks in the males and also for the presence of tusks in both sexes of Dugong. The former will be dealt with here, but the latter will be considered in a later section of this chapter on the origin of Dugong.

It would be very easy to suggest that the tusks are retained in the male because they might be useful in intraspecific combat, but no definite cases of such use have been observed in Dugong. Annandale (1905) concluded, from the presence of scars, that the males fight with their tusks during the breeding season, but Fernand (1953) dismissed these scars as being caused by sharp pieces of coral and shell. Kingdon (1971) stated that males have been known to defend their mates and young against hunters, but he did not say if they used their tusks in such situations. Since the tusks of the male dugong cannot have any important function in relation to nutrition (Owen, 1845) and since there have been no authenticated cases of their use as weapons, it is an open matter as to how they are utilized. However, because little work has been carried out on the dugong in the wild it may only be because of inadequate observation that the true purpose of the tusks has been missed.

THE GENUS HALITHERIUM KAUP

The most abundant and best preserved remains of the dugongid genus Halitherium have been found in the Palaeogene sedimentary basins of northern Europe, especially the Aquitaine, Mainz, and Linz Basins. The type species, Halitherium schinzi Kaup 1838, was described from Stampian (Lower Oligocene) sediments of the Mainz Basin, and since its discovery numerous other sirenian remains have been referred to this genus. H. schinzi has now been recorded from Lower Oligocene strata in France, Switzerland, Belgium, and Italy as well as the classic area around Mainz. A second species, H. chouqueti, was later described from the Stampian of the Paris Basin (Gaudry, 1884), but it is only known from ribs and is most probably synonymous with H. schinzi.

The genus extends into the Chattian (Upper Oligocene), and four species are recognized with certainty from this level - three from the Linz Basin of Austria and one from northern Italy. The Linz sirenians have been ably studied by Spillmann (1959), who arranged them in a phylogenetic sequence (H. pergense → H. christoli → H. abeli) that can be linked to the Lower Oligocene Halitherium species by H. pergense and to the Lower Miocene (Burdigalian) Metaxytherium krahuletzi by H. abeli (see Table 11). H. bellunense has been described from northern Italy (de Zigno, 1875) in deposits that have been placed in the Chattian by dal Piaz (1937).

The presence of Halitherium in pre-Oligocene rocks cannot be ruled out because Halitherium-like skull roofs have been found in the Eocene of Hungary and Romania (Kretzoi, 1941; Fuchs, 1970). The only verified post-Oligocene occurrence of the genus is some material from Florida that Dr. R. H. Reinhart (pers. comm.) believes is at the same stage of evolution as the European Oligocene forms, but which comes from a Middle-Late Miocene stratum.

Therefore, in Europe at least, Halitherium is restricted to the Oligocene, but problems arise when inadequate sirenian remains are described from areas away from the classic European sites and are referred to this genus. Five good examples of this practice are H. schinzi ? from the Maltese islands (Adams, 1866, 1870, and 1879), H. canhami from Suffolk, England (Flower,

1874), H.? antillense from Puerto Rico (Matthew, 1916), H. sp. from the Malagasy Republic (Collignon & Cottreau, 1927), and H.(?) sp. from Congo (Dartevelle, 1935).

Halitherium schinzi ? from the Maltese islands

A number of assorted sirenian remains from Malta and Gozo have been reported by Adams (1866, 1870, and 1879) under the name H. schinzi ?. The remains, including teeth, have come from various geological formations on the two islands, and up until now no doubt has been cast on their generic identification. In the last of his three papers (1879), Adams lists the sirenian remains from Malta and Gozo, and he allocates all of them to the Miocene. A shortened version of Adams' list is given below together with a revised stratigraphical nomenclature that is taken from House, Dunham, & Wigglesworth (1961):

'1. A molar from a nodule bed of Calcareous Sandstone (=Globigerina Limestone of House et al.), and an "ear-bone".....with several caudal vertebrae, from the Sand bed (=Greensand of House et al.).
2. ...a similar tooth (possibly a penultimate true molar)..., from the Lower Limestone (=Lower Coralline Limestone of House et al.).
3. ...a fragment of a jaw with two teeth in situ.....found in Gozo.
4. ...broken crown.....from the Sand bed (=Greensand of House et al.) in Gozo.
5. Several vertebrae.....with fragments of ribs.....from the marl and nodule seams of the Calcareous Sandstone (=Globigerina Limestone of House et al.).' (Adams, 1879)

House et al. (1961) correlate the Maltese formations thus:

TABLE 10

FORMATION	STAGE
Upper Coralline Limestone	Tortonian
Greensand *	Helvetian
Blue Clay Globigerina Limestone *	Burdigalian
Lower Coralline Limestone *	Aquitanian

* sirenian remains

Therefore the Maltese sirenians have a wide range from the Aquitanian to the Helvetian (= Burdigalian-Langhian). One of the five teeth is unfortunately too worn to be of use as a generic indicator, and the remaining four are barely adequate for comparison purposes. Spillmann (1959) gave a table listing the main anatomical differences between Halitherium and the Miocene genus Metaxytherium - one of the main characters being that the anterior cingulum of a Halitherium molar is composed of a number of small tubercles, whereas in Metaxytherium it takes the shape of a large accessory cusp that is inserted between the protocone and the protoconule. The maxillary fragment from an unidentified horizon on Gozo (Adams, 1879) contains an almost complete M^1 and M^2 that, because of their size and the absence of a tuberculate anterior cingulum, should be referred to Metaxytherium rather than to Halitherium. The broken enamel crown that Adams (ibid.) suggested was an M_2 is more probably an M_3 and its size, together with its Miocene age, point to Metaxytherium and not Halitherium.

There is therefore no legitimate reason for including any of the Maltese sirenians in the species Halitherium schinzi, and it would be more sensible to attribute the remains to Metaxytherium spp. indet.. This reorganization does not create a problem in Miocene sirenian distribution because the latter genus is already recorded from the Helvetian of Sardinia (Caria, 1957).

Halitherium canhami from Suffolk, England

Sirenian remains were first reported from the bonebed at the base of the Pliocene Red Crag at Foxhall, Suffolk, by Flower (1874), who used a very badly worn skull fragment from the collection of the Rev. H. Canham as the basis of a new species, Halitherium canhami. Flower believed that the Crag sirenian was very similar to, but larger than, H. schinzi from the Miocene (sic.) of the Rhine Valley. Sickenberg (1934) removed this specimen from the genus Halitherium and synonymized it with Miosiren kocki Dollo, of which good material was recorded from the Upper Miocene rocks of Belgium. Sickenberg (ibid., p. 333) stated:

'Es geht schon aus der Beschreibung und aus den Abbildungen klar hervor, dass "Halitherium" canhami zu Miosiren gehören muss, ja es besteht die grösste Wahrscheinlichkeit, dass diese Form sogar artgleich mit M. kocki ist.'

Sickenberg only had a cast of the Suffolk skull fragment to compare with the skull of M. kocki, but he could find no appreciable differences between the two individuals. He indicated that Flower was misled as to the number of alveoli in the broken maxillae because extra depressions and pits had appeared in this region during fossilization - a feature that is common to many fossils from this particular bonebed.

Recent evidence (Hooyberghs & de Meuter, 1972) shows that the Edegem Sands, Belgium, from which M. kocki is recorded, contain a foraminiferan fauna that is characteristic of Zone P20/N1 i.e. Early-Late Oligocene in age (Berggren, 1972). This new date agrees much better with the stage of evolution of M. kocki than does the Late Miocene age proposed by Sickenberg (1934).

Newton (1891) referred a right M^3 from the Red Crag Nodule-bed of Felixstowe, Suffolk, to Flower's species (H. canhami), but having seen this specimen in York Museum I believe that it cannot belong either to a species of Halitherium or to Miosiren kocki. M. kocki can be eliminated because one of its characteristic features is a very reduced and flattened M^3 that is very unlike the bilophodont tooth in question. Although the M^3 from Felixstowe is worn there is no indication of the tuberculate anterior cingulum that is characteristic of Halitherium, and the absence of this feature, together with the large size of the tooth, indicate a relationship with the Metaxytherium-Felsinotherium complex.

The presence of two stratigraphically distinct sirenian genera in the Nodule-bed need not cause too much concern because it is well known that many of the fossils from this bed are derived from older deposits (Newton, 1891). However, precise identification of the genera present must depend upon the discovery of less worn and more complete material.

Halitherium? antillense from Puerto Rico

Matthew (1916) described a broken mandible and two vertebrae from Puerto Rico as a new species of sirenian, Halitherium? antillense. These specimens were found in calcareous shales that have since been placed in the Juana Diaz Formation, the precise age of which has been the subject of some controversy. Cooke, Gardner, & Woodring (1943) placed the Juana Diaz Formation in the Middle Oligocene, although Gordon (1961) indicated that it was the southern equivalent of the lower part of the San Sebastian Formation (Aquitanian). However, van den Bold (1965) has dated the upper part of the San Sebastian Formation as Late Oligocene, and Moussa & Seiglie (1970) have given the Juana Diaz Formation a similar age.

Reinhart (1959) referred to the fact that Matthew's specimens did not show any characters of generic distinction. Until better material is available it is advisable to consider H.? antillense as an indeterminate Oligocene dugongid rather than to assign it to a definite genus or species.

Halitherium sp. from the Malagasy Republic

The only Neogene sirenian recorded from the east coast of Africa is a small species represented by a broken cranium and other skull fragments from the Miocene (Burdigalian-Helvetian) of Ile Makamby, Malagasy Republic (Collignon & Cottreau, 1927). Because of its small size the principal specimen was thought to belong to a young individual, and the disposition of its temporal crests was believed to indicate a species of Halitherium. The only other material recovered with the skull fragments consisted of broken ribs and these confirmed the small size of the individual. The size and shape of the temporal crests cannot be used as a reliable feature to distinguish Halitherium from other dugongid genera because the crests exhibit pronounced intrageneric differences. The absence of the characteristic nasal region makes it impossible to allocate the Ile Makamby sirenian to a definite genus, and it is best considered incertae sedis within the Dugongidae.

TABLE 11 Range of Halitherium and Metaxytherium

MIOCENE	LANGHIAN	M. medium : M. lovisatoi
	BURDIGALIAN	M. beaumonti : M. studeri : M. krahuletzi : M. meyeri
	AQUITANIAN	?
OLIGOCENE	CHATTIAN	H. abeli H. bellunense : H. christoli H. pergense
	RUPELIAN	H. chouqueti : H. schinzi

Halitherium (?) sp. from Congo

Sirenian ribs from Malembe, Congo, have been referred to Halitherium (?) sp. (Dartevelle, 1935), but there is no other material to substantiate this claim. Since the associated fauna suggests a Burdigalian age for this western Congo site, these sirenian remains are older than those of any European Halitherium, but are within the stratigraphic range of Metaxytherium. Although the ribs of sirenians are diagnostic for the order, they cannot be successfully used for the identification of lower taxa and so the Congo sirenian should be regarded as indeterminate.

THE GENUS METAXYTHERIUM (DESMAREST)

There has been much discussion about whether the genera Metaxytherium and Halianassa are morphologically distinct. The type species of the latter genus, H. studeri Studer, may be identical with Metaxytherium beaumonti de Christol or M. krahuletzi Depéret (Depéret & Roman, 1920), and Domning (1970a) has synonymized Halianassa vanderhoofi Reinhart with Metaxytherium jordani Kellogg. Simpson (1932) realized that the two forms were very similar, although he believed that Halianassa was the prior and valid name; however, Kellogg (1966) has ably shown that Metaxytherium is in fact the correct name and I intend to include all of the species referred to Halianassa in that genus.

Metaxytherium is known with certainty from the Miocene deposits of Europe and the Americas. Apart from a premature occurrence in Baja California (Kilmer, 1965), the genus is first recorded in the Burdigalian of central Europe. M. krahuletzi and M. meyeri Abel are known from the Burdigalian of Austria and Germany respectively; the first species may be identical with M. beaumonti from southern France and M. (=Halianassa) studeri from Switzerland. The specimens referred to these four species must be critically re-examined to determine whether there are any diagnostic characters to

support this rapid diversification in such a short period of time. Incomplete sirenian remains from Burdigalian strata that may belong to Metaxytherium include teeth from Malta and Gozo (see above) and post-cranial remains from Hungary (Koch, 1903).

Only two species of Metaxytherium occur in the Helvetian (=Burdigalian-Langhian) of Europe, and they have a more restricted range than their ancestors. The type species, M. medium (Desmarest) (=M. cuvieri de Christol), is a very common fossil in the Loire Basin, France, and it also occurs, with M. lovisatoi Capellini, on Sardinia. Some ribs found in the Middle Fars Limestone (Upper Miocene) of Iran may represent an eastward extension of the range of this genus.

No recognizable remains of Metaxytherium are known from the Late Miocene of Europe, although other genera are present. Some bones, including a worn right M^3, from an Upper Miocene level in a quarry near Eibergen, Holland, have been ascribed to Halianassa (=Metaxytherium), but more material needs to be found before this identification can be verified (author's notes). A sirenian rib cage has been found in the Upper Miocene Gerani Formation of Crete by Dr. P. Y. Sondaar (pers. comm.), but unfortunately the skull was not present and identification was impossible.

The American representatives of the genus are known from both east and west coasts. The earliest appearance of Metaxytherium on the American continent is surprisingly on the west coast, Halianassa(?) (=Metaxytherium) allisoni from Baja California, Mexico (Kilmer, 1965). This species is based on a broken mandible collected from the Ysidro Formation (Lower-Middle Miocene), but Domning (pers. comm.) has found new material that can be assigned to this species. The Ysidro Formation has also yielded remains belonging to an immature individual of a larger sirenian species that Reinhart (1959) identified as Halianassa (=Metaxytherium) sp. indet.. The presence of Metaxytherium in Mexico at such an early period in time raises some problems, but it is hoped that the newly obtained material will help to dispel these.

The Middle Miocene forms of Metaxytherium are so far restricted to the east coast, extending from Florida in the south to as far north as Maryland. The best known species is M. calvertense Kellogg from the Middle Miocene Calvert Formation of Maryland (Kellogg, 1966), the type specimen of which is the almost complete skeleton of an immature sirenian. Metaxytherium (=Hesperosiren) crataegensis (Simpson) has been allocated to this genus because of the reasons outlined in the first section of this chapter. It is only known from the Hawthorn Formation of Quincy, Florida (Simpson, 1932). Metaxytherium (=Dioplotherium) manigaulti (Cope) is a large sirenian that is represented by broken remains dredged from the Wando River, South Carolina (Kellogg, 1966); unfortunately it is not possible to date these deposits accurately because they contain a large number of remanié fossils.

The two Upper Miocene American species are found on the west coast - one in California and the other in Colombia. M. jordani (including Halianassa vanderhoofi) is recognized from Santa Barbara County (Kellogg, 1925) and Santa Cruz County (Reinhart, 1959), California, and Domning (1971) believes that it is directly ancestral to the Plio-Pleistocene genus Hydrodamalis. The only record in the literature of a dugongid from South America is that reported by Kellogg (1966) from the Honda Formation of Colombia. This species, M. ortegense Kellogg, is known with certainty only from a left maxilla containing three teeth. However, the mandible previously referred to Potamosiren magdalenensis Reinhart in all probability belongs to a dugongid, but a more accurate identification is not possible (see Chapter 3). Reinhart (pers. comm.) has an isolated sirenian tooth from the Middle-Upper Miocene of Argentina that is awaiting description, but which he says belongs to Metaxytherium.

Three Miocene genera have been erected on the basis of insufficient evidence and it is possible that at least one of these can be placed in Metaxytherium. The species in question are Miodugong brevicranius from Ceylon (Deraniyagala, 1969), Prohalicore dubaleni from France (Flot, 1887),

and Haplosiren leganyii from Hungary (Kretzoi, 1951).

Miodugong brevicranius Deraniyagala

A skull fragment from the Miocene Malu member of Ceylon forms the basis of this genus (Deraniyagala, 1969). The only reason for erecting a new genus on such scanty material was the fact that it was the first record of a Miocene sirenian from the Indian subcontinent. Since Miocene sirenian remains are now known from Madagascar (Collignon & Cottreau, 1927), Iran (author's notes), Java (von Koenigswald, 1952), and northwestern India (R. J. G. Savage, pers. comm.), it is evident that the order had a wide, though poorly recorded, distribution in the Indian Ocean area. Deraniyagala recognized the similarity of his material to that of Halianassa (=Metaxytherium), and I recommend the transference of the specimens in question to Metaxytherium sp. indet. until more adequate material is available.

Prohalicore dubaleni Flot

The broken mandible of P. dubaleni, from the Helvetian (=Burdigalian-Langhian) of Audon, France, is characterized according to Flot (1887) by its elongation and the cylindrical shape of its horizontal ramus. These features may be accentuated in this specimen because the alveolar border is very broken and the vertical ramus is missing. No information can be obtained from the dentition because all that remains are the roots of the anterior teeth. The dentition is not as reduced as in contemporaneous species because it appears that three premolars were retained. Because of these characters Depéret and Roman (1920) thought that Prohalicore could be a Miocene descendant of Eotheroides libycum, but this is unlikely because no intermediate forms are known. When better material has been found it may be possible to derive Prohalicore from one of the French species of Metaxytherium, but until then it is best left as an indeterminate dugongid.

Haplosiren leganyii Kretzoi

Hungary has yielded some tantalizing though fragmentary sirenian remains, mainly due to the assiduousness of Kretzoi: Haplosiren leganyii is no exception. Kretzoi (1951) described a mandibular fragment containing M_2 and M_3 from the Tortonian (Upper Miocene) of Mátraszöllős, Hungary, as representative of a new genus, Haplosiren. He noted that it was a large sirenian with the talonid of the lower molars reduced to a single cusp. Kretzoi believed that Haplosiren was intermediate between Metaxytherium and Felsinotherium, but since the last two genera may be synonymous it is best to regard the sirenian from Mátraszöllős as an indeterminate metaxytheriine until better material is available.

THE ORIGIN OF DUGONG

The most comprehensive survey of the literature concerning the origin of the Dugonginae was that produced by Simpson (1932). He reviewed the relevant publications and came to the conclusion that Dugong arose from "late Tertiary Halitheriinae structurally similar to the known forms allied to Metaxytherium or Felsinotherium" - it must be remembered that when Simpson wrote this the subfamily Halitheriinae contained Metaxytherium and Felsinotherium as well as the type genus. Some of the early authors (Abel, 1904, 1919; Depéret & Roman, 1920) had doubts about putting Dugong as a direct descendant of the large Pliocene sirenians (Felsinotherium), but Simpson assessed the evidence and believed that Dugong could satisfactorily be derived from one of these late species. I will now present new evidence for the origin of Dugong, taking into account the unusual features of its dentition and the latest palaeontological information from the Indian Ocean area.

Differences exist between both the symphysial and cheek teeth of Dugong

and those of other Cenozoic sirenians. It was outlined above why there are reasons for considering the majority of tuskless dugongids to be females, and it was stated that one of the barriers to this suggestion was the presence of tusks in female dugongs. This barrier is only effective if Dugong is considered as a direct continuation of the Metaxytherium-Felsinotherium lineage; since tusklessness is assumed in this group from the Middle Miocene onwards, it would be extremely unlikely for enlarged incisors to reappear in later forms. However, if the origin of Dugong is taken as pre-Middle Miocene then this obstacle to tusklessness is removed. Can this early origin for the Dugonginae be supported by the new information that has accumulated since Simpson's paper?

The earliest sirenian genus that bears a close morphological resemblance to Dugong is Metaxytherium, which makes its first appearance in the Lower Miocene of France, Germany, and Austria, and is a common fossil in some of the marine deposits along the northern shore of Tethys. This genus is almost identical to the later Felsinotherium and is just as advanced in skeletal characters as the latter. Thus there is no anatomical reason why the Miocene Metaxytherium could not be the ancestor of Dugong. Dugong is markedly different from both Metaxytherium and Felsinotherium in the structure of its cheek teeth. The teeth of the Metaxytherium-Felsinotherium group are lophodont and enamelled, but those of Dugong are very quickly worn to produce a flat occlusal surface because they only have a thin enamel layer that is lost as soon as each tooth comes into use (Fernand, 1953). This major adaptation of the dentition is unlikely to have taken place during such a short period as that represented by late Pliocene-Recent. Although the adult dugong only retains two molar teeth in each half of the jaw, it has been shown that a total of five or six teeth do appear during the life of the animal (Fernand, ibid.). This observation indicates that Dugong arose from an early ancestor because the late metaxytheriines only have four cheek teeth in each half of the jaw.

The palaeogeography of the Miocene can be used as evidence for the origin of Dugong. It is believed that during the Palaeogene the Tethyan and Indo-Pacific regions were connected by a seaway, but that this connection was blocked by Middle Miocene times. This hypothesis is supported by foraminiferal and ostracod information (Adams, 1967; McKenzie, 1967), and also by the fact that intercontinental migration of mammals was very significant from the Middle Miocene onwards (Van Couvering, 1972). If the ancestor of Dugong entered the Indo-Pacific region from Tethys before the Middle Miocene it would be effectively isolated from the rest of the metaxytheriine stock from then on. The barrier between the two areas would stop the intermingling of sirenian populations as effectively as it stopped the mixing of distinct groups of foraminiferans and ostracods. Once a group of sirenians was thus isolated it could evolve independently of the other population centres in the Mediterranean and Atlantic areas.

The palaeontological evidence for the early presence of sirenians in the Indian Ocean region is sparse and inconclusive, consisting of fragments from five widely separated localities: Ile Makamby, Malagasy Republic (see section on the genus Halitherium); Iran (see section on the genus Metaxytherium); Kutch; Ceylon (see section on the genus Metaxytherium); and Java. The Upper Miocene rocks of Java have yielded an isolated molar that von Koenigswald (1952) identified as sirenian in origin. He created a new genus, Indosiren, for this specimen, which I would prefer to leave incertae sedis because it is probably a deciduous tooth. When von Koenigswald compared this tooth with those from other Cenozoic sirenians, he came to the conclusion that it most closely resembled the last upper deciduous molar of Prototherium from the Upper Eocene. The most complete material from Asia is awaiting description and consists of teeth and parts of a skull of a large metaxytheriine from western Kutch (R. J. G. Savage, pers. comm.). Since the geological age of this material is in doubt, it is not possible to make a precise identification yet.

All of these occurrences are in rocks of Miocene (or Pliocene?) age and show that the metaxytheriines, at least, penetrated as far east as northern India. It is not possible to identify an ancestor of Dugong in this poor assemblage because so far the specimens have been too fragmentary. It is necessary to have much more complete material from Miocene and Pliocene localities in Asia before any more definite relationships can be formulated.

Shikama & Domning (1970) reported the finding of a rib of Hydrodamalis in upper Pliocene strata in central Japan, and they believed that this genus could be derived from Metaxytherium jordani of the Californian Late Miocene. The possibility of Dugong having entered the Indo-Pacific area via the Pacific coast of North America is very unlikely because the Californian metaxytheriines were already very specialized.

THE IMPORTANCE OF TETHYS IN THE ORIGIN AND EVOLUTION OF THE SIRENIA

On the basis of the distribution of fossil and living sirenians it is possible to divide the globe into four large marine provinces: a European Province (including the North Sea Basin, the Atlantic and Mediterranean basins, and the eastern European basins); a West Atlantic Province (including the Caribbean, and the east coasts of southern North America and northern South America); a North Pacific Province (including the west coasts of North America and northern South America, and the east coast of northern Asia); and an Indo-Pacific Province (extending from the east coast of Africa across the Indian Ocean, and through Indonesia to the southwestern Pacific). Only one of the 40-odd species recognized in this thesis has a range that is wholly outside of these provinces - Trichechus senegalensis (Link) has, in the recent past, crossed the Atlantic Ocean from the West Atlantic Province to the rivers of the west coast of Africa.

The earliest known sirenian remains have been found in Ypresian-lower Lutetian strata in Romania (Grigorescu, 1967), although by the Late Eocene

primitive sirenians are also to be found in other parts of the European Province and in the West Atlantic and Indo-Pacific Provinces. The priority in time of the Romanian specimen suggests that the Sirenia may have originated in the area of what is now southeastern Europe. Unfortunately the material is very scanty and, although it is certainly sirenian (pachyostosed rib fragments), no more accurate identification is possible.

The European Province contains by far the largest number of fossil sirenian localities, but it must be stressed that these result from the intensive geological and palaeontological investigations that have been carried out in this region. These investigations have also been responsible for the profusion of taxa recorded from the European Province. Parts of the West Atlantic and North Pacific Provinces have rewarded recent work by yielding new localities and taxa, but the Indo-Pacific Province still awaits detailed exploration by the vertebrate palaeontologist.

Each province contains a number of endemic genera and species, and only four out of the nineteen recognized sirenian genera are known to occur in more than one province - Halitherium, Metaxytherium, Felsinotherium, and Dugong. Even more striking is the fact that only one species is recorded from more than one province - Dugong dugon (Errleben). It is significant that the percentage of endemic taxa to total number of taxa is highest in the European Province (see Table 12c). Present evidence indicates that the three fossil genera that are common to more than one province first appear in the European Province and then spread out into the other provinces. Of course, this will only be verifiable when more accurate trans-Atlantic correlations are available. The three pandemic genera seem to have crossed the Atlantic independently, but their European and American species require closer comparison before a definite decision can be made. The movement of sirenians into the Indo-Pacific Province was dealt with in the previous section.

The sirenians, like the other subungulate groups, most probably have their origins within the Condylarthra. However, Van Valen (1971) made the equivocal statement that the subungulates could possibly be derived from "...an animal that would be called a perissodactyl (although it would

TABLE 12

NUMERICAL ANALYSES OF SIRENIAN GENERA AND SPECIES

19 genera of sirenians are recognized in this work - 15 are endemic

44 species of sirenians (excluding *Trichechus senegalensis*) are recognized in this work - 43 are endemic.

a. Number of taxa in each province

	Genera	Species
European Province	12	26
West Atlantic Province	8	13
North Pacific Province	3	5
Indo-Pacific Province	2	1

b. Number of endemic taxa in each province (also expressed as percentage of total number of endemic taxa)

	Genera	Species
European Province	9 (60%)	26 (60%)
West Atlantic Province	5 (33%)	13 (30%)
North Pacific Province	1 (7%)	4 (10%)
Indo-Pacific Province	0	0

c. Percentage of endemic taxa in each province ($\frac{b}{t}$)

	Genera	Species
European Province	75%	100%
West Atlantic Province	63%	100%
North Pacific Province	33%	80%
Indo-Pacific Province	0%	0%

probably not be called Hyracotherium)...". Possible sirenian ancestors existed on mainland Europe during the Palaeogene in the form of phenacodontid and meniscotheriid condylarths (e.g. Pleuraspidotherium). Pleuraspidotherium shows certain similarities to the earliest sirenians in basic skull morphology, especially in the temporal region (e.g. no ossified tympanic, longitudinal crest on petrosal, stout post-tympanic process). No condylarths have yet been discovered in Africa, where the subungulate orders are very prominent in the Eocene and Oligocene faunas.

A NEW SIRENIAN CLASSIFICATION

Sirenian classification since Simpson (1945)

The classification of the Sirenia used by Simpson (1945) in his classification of mammals was a modified version of an earlier system (Simpson, 1932). The modifications were principally restricted to the Eocene sirenians and were necessitated by Sickenberg's (1934) review of that part of the order. Simpson (1945) divided the Sirenia into two suborders, the Trichechiformes and the Desmostyliformes - the former contained all of the true sirenians, whereas the latter was restricted to the extraordinary desmostylids. The true sirenians were subdivided into four families: Prorastomus and Protosiren were both placed in monotypic families; Dugong and its ancestors (including Eotheroides, Prototherium, and several divergent stocks) comprised a third family, the Dugongidae, which had five subfamilies; and the manatee, Trichechus, was put into another monotypic family. The desmostylids, although placed in the Sirenia, were recognized by Simpson to be most probably highly aberrant offshoots of that order.

Reinhart (1953) diagnosed the new mammalian order Desmostylia, which removed Desmostylus and Cornwallius from the list of sirenian genera. The next classification of the Sirenia (Dechaseaux, 1958) was therefore the same

as Simpson's except for the exclusion of the Desmostyliformes (and therefore the absence of suborders).

The most recent reviewer of the sirenians (Reinhart, 1959) has drastically revised their classification and has recognized only two families; the Dugongidae containing all of the Eocene forms plus Dugong and its allies, and the Trichechidae containing just Potamosiren and Trichechus. Reinhart relegated two of Simpson's and Dechaseaux' families to the status of subfamilies within the Dugongidae, and enlarged one of these to include Eotheroides and Sirenavus as well as the type genus, Prorastomus. He also removed some genera from the dugongid subfamily Halitheriinae to form the new subfamily Halianassinae.

New sirenian classification

The new classification proposed below (re)introduces the following features:

1. promotion of the Prorastominae to family rank and its restriction to Prorastomus
2. promotion of the Protosireninae to family rank and the inclusion of Libysiren as well as Protosiren
3. erection of a new family, the Eotheroididae, to include Eotheroides and Prototherium
4. inclusion of these three families in a new superfamily, the Prorastomoidea
5. inclusion of the Trichechidae and the Dugongidae in new separate superfamilies, the Trichechoidea and the Dugongoidea respectively, to emphasize the differences between them and the Prorastomoidea

Order SIRENIA Illiger 1811

Diagnosis: Aquatic mammals. Premaxillae form a rostrum that is deflected in later forms; external nares dorsal; nasals prominent in primitive forms, but decrease in size as the mesorostral fossa enlarges; periotic isolated from

rest of braincase in all genera except Prorastomus; tympanic semicircular. Number of incisors becomes progressively reduced; cheek teeth primitively bilophodont, but show great morphological variation in the different subfamilies. Hind limbs become reduced and functionless; fore limbs become paddle-like. Tail with horizontal fluke. M. Eocene-Recent

Superfamily PRORASTOMOIDEA superfam. nov.

Diagnosis: Rostrum slightly deflected; large nasals form anterior part of skull roof. Complete eutherian dental formula; incisor tusks begin to enlarge in some genera. Hind limbs function as paddles. M.-U. Eocene

Family PRORASTOMIDAE Cope 1889

Diagnosis: Periotic still attached to braincase. No enlarged incisor tusks. M.(?) Eocene

Prorastomus Owen 1855

Family PROTOSIRENIDAE Sickenberg 1934

Diagnosis: Lacrimal foramen and duct absent (at least in Libysiren); alisphenoid canal present; elongated superficies meatus; processus fonticulus present; periotic isolated from rest of braincase. Incisor tusks beginning to enlarge. M. Eocene

Protosiren Abel 1904
Libysiren gen. nov.

Family EOTHEROIDIDAE fam. nov.

Diagnosis: Lacrimal foramen and duct present; alisphenoid canal absent; short superficies meatus; processus fonticulus absent; periotic isolated from rest of braincase. Incisor tusks beginning to enlarge. M.-U. Eocene

Eotheroides Palmer 1899
Prototherium de Zigno 1887

Superfamily TRICHECHOIDEA superfam. nov.

Diagnosis: Rostrum small and little deflected. Numerically increased dentition; incisor tusks absent; cheek teeth continuously replaced from rear.

No bicipital groove on humerus; carpals little fused; hind limbs reduced and functionless; ilium greatly reduced or absent; ischium relatively large and triangular. Six cervical vertebrae; usually seventeen thoracic vertebrae.

L. Miocene-Recent

Family TRICHECHIDAE Gill 1872

Diagnosis: As for superfamily.

Trichechus Linnaeus 1758
Ribodon Ameghino 1883
Sirenotherium Paula Couto 1967

Superfamily DUGONGOIDEA superfam. nov.

Diagnosis: Rostrum enlarged and deflected. Numerically reduced dentition; incisor tusks usually present (at least in the male); premolars disappear in advanced genera. Broad bicipital groove on humerus; carpals tend to become fused; hind limbs reduced and functionless; ilium becomes rod-like. Seven cervical vertebrae; usually nineteen to twenty thoracic vertebrae.

L. Oligocene-Recent

Family DUGONGIDAE Gray 1821

Diagnosis: As for superfamily.

Subfamily HALITHERIINAE Abel 1913

Diagnosis: Rostrum strongly deflected; nasals join in mid-line. Incisor tusks usually present; cheek teeth enamelled; M^3 unreduced and complex.

L. Oligocene-M. Miocene

Halitherium Kaup 1838
Anomotherium Siegfried 1965
Thalattosiren (Abel 1904)

Subfamily MIOSIRENINAE Abel 1919

Diagnosis: Rostrum deflected; occiput broad and cranium rounded; supra-occipital reaching foramen magnum. Large incisor tusks present; cheek teeth enamelled; M^3 much reduced with a simple pattern. L.-U. Oligocene

Miosiren Dollo 1889

Subfamily RYTIODINAE Abel 1928

Diagnosis: Rostrum strongly deflected; large lacrimal bone, but no lacrimal duct; narrow parietals. Large, flattened incisor tusks; cheek teeth enamelled; M^3 unreduced and complex. L. Miocene

Rytiodus Lartet 1866

Subfamily METAXYTHERIINAE subfam. nov.

Diagnosis: Rostrum strongly deflected; nasals separated in mid-line by frontals. Incisor tusks present (in adult males only?); cheek teeth enamelled; M^3 unreduced and complex. U. Oligocene(?)-Pliocene

Metaxytherium de Christol 1840
Felsinotherium Capellini 1871
Caribosiren Reinhart 1959 (?)

Subfamily HYDRODAMALINAE Simpson 1932

Diagnosis: Rostrum large, narrow, and moderately deflected; nasals small and separated in mid-line by frontals. No functional teeth. Pliocene-Recent

Hydrodamalis Zimmermann 1780

Subfamily DUGONGINAE Simpson 1932

Diagnosis: Rostrum strongly deflected; vestigial nasals separated by frontals; supraoccipital reaches foramen magnum. Large upper incisor tusks in male; cheek teeth without enamel and with open roots; only two cheek teeth in each half of jaw of adult. Recent

Dugong (Müller 1776)

INCERTAE SEDIS

Sirenavus Kretzoi 1941

SELECTED BIBLIOGRAPHY

ABEL, O. 1904. Die Sirenen der mediterranen Tertiarbildungen Österreichs. Abh. geol. Reichsanst., Wien, 19, 2. vi + 223pp.

ABEL, O. 1913. Die eocänen Sirenen der Mittelmeerregion. Erster Teil: Der Schädel von Eotherium aegyptiacum. Palaeontographica, 59: 289-363.

ABEL, O. 1919. Die Stämme der Wirbeltiere. xviii + 914pp. Berlin.

ABEL, O. 1928. Vorgeschichte der Sirenia. In Weber, M. Die Säugetiere. 2. 2nd ed: 496-504.

ADAMS, A.L. 1866. On the discovery of remains of Halitherium in the Miocene deposits of Malta. Q. Jl geol. Soc. Lond., 23: 595-596.

ADAMS, A.L. 1870. Notes of a naturalist in the Nile Valley and Malta. 295pp. Edinburgh.

ADAMS, A.L. 1879. On remains of Mastodon and other Vertebrata of the Miocene beds of the Maltese islands. Q. Jl geol. Soc. Lond., 35: 517-531.

ADAMS, C.G. 1967. Tertiary foraminifera in the Tethyan, American, and Indo-Pacific provinces. In Adams, C.G. & Ager, D.V. (Eds). Aspects of Tethyan Biogeography. Publs Syst. Ass., 7: 195-217.

AMEGHINO, F. 1883. Sobre una colección de mamíferos fósiles del piso mesopotámico de la formación patagónica. Boln Acad. nac. Cienc. Córdoba, 5: 101-116.

ANDREWS, C.W. 1902. Preliminary note on some recently discovered extinct vertebrates from Egypt. (Part 3). Geol. Mag., (4) 9: 291-295.

ANDREWS, C.W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. xxxvii + 324 pp. London.

ANNANDALE, N. 1905. Notes on the species and external characters of the dugong (Halicore dugong). J. Asiat. Soc. Beng., 1: 238-243.

ARAMBOURG, C. 1961a. Prolibytherium magnieri, un vellericorne nouveau du Burdigalien de Libye. C. r. Séanc. Soc. géol. Fr., 3: 61-62.

ARAMBOURG, C. 1961b. Note préliminaire sur quelques Vertébrés nouveaux du Burdigalien de Libye. C. r. Séanc. Soc. géol. Fr., 4: 107-108.

ARAMBOURG, C. 1963a. Continental vertebrate faunas of the Tertiary of North Africa. In Howell, F.C. & Bourliere, F. (Eds). African ecology and human evolution: 55-64. Chicago.

ARAMBOURG, C. 1963b. Le genre Bunolistriodon Arambourg 1933. Bull. Soc.

géol. Fr., (7) 5: 903-911.

ARAMBOURG, C. & MAGNIER, P. 1961. Gisements de Vertébrés dans le bassin tertiaire de Syrte (Libye). C. r. hebd. Séanc. Acad. Sci., Paris, 252: 1181-1183.

ARNOULD-SAGET, S. & MAGNIER, P. 1961. Découverte de dents de Palaeomastodontes dans la région de Zella (Tripolitaine). Bull. Soc. géol. Fr., (7) 3: 283-286.

BEADNELL, H.J.L. 1905. The topography and geology of the Fayum Province of Egypt. 101pp. Cairo.

BERGGREN, W.A. 1967. Biostratigraphy and planktonic foraminiferal zonation of the Tertiary system of the Sirte basin of Libya, north Africa. Int. Conf. Planktonic Microfossils, 1st. Proc., 1: 104-120.

BERGGREN, W.A. 1971. Tertiary boundaries and correlation. In Funnell, B.M. & Riedel, W.R. The micropalaeontology of oceans: 693-809. Cambridge.

BERGGREN, W.A. 1972. A Cenozoic time-scale - some implications for regional geology and paleobiogeography. Lethaia, 5: 195-215.

BERTRAM, C.K.R. & BERTRAM, G.C.L. 1968. The Sirenia as aquatic meat-producing herbivores. Symp. zool. Soc. Lond., 21: 385-391.

BISHOP, W.W., MILLER, J.A. & FITCH, F.J. 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. Am. J. Sci., 267: 669-699.

BOLD, W.A. van den. 1965. Middle Tertiary Ostracoda from northwestern Puerto Rico. Micropaleontology, 11: 381-414.

CARIA, I.C. 1957. Nuovi resti di sirenii nel Miocene della Sardegna. Boll. Soc. geol. ital., 76: 288-301.

CICHA, I. 1970. Stratigraphical problems of the Miocene of Europe. Rozpr. ústřed. Úst. geol., 35. 134pp.

COLLIGNON, M. & COTTREAU, J. 1927. Paléontologie de Madagascar. 17: Fossiles du Miocène marin. Annls Paléont., 16: 135-171.

COOKE, C.W., GARDNER, J. & WOODRING, W.P. 1943. Correlation of the Cenozoic formations of the Atlantic and Gulf Coastal Plain and the Caribbean region. Bull. geol. Soc. Am., 54: 1713-1723.

COPE, E.D. 1869. Synopsis of the extinct Mammalia of the cave formations in the United States, with observations on some Myriapoda found in and near the same, and on some extinct mammals of the caves of

Anguila etc.. Proc. Am. phil. Soc., 11: 171-192.

COPE, E.D. 1883. On a new extinct genus of Sirenia from South Carolina. Proc. Acad. nat. Sci. Philad., 35: 52-54.

COTTREAU, J. 1928. Le Metaxytherium cuvieri du golfe de la Loire. Annls Paléont., 17: 3-20.

DARTEVELLE, E. 1935. Les premiers restes de mammifères du tertiaire du Congo; la faune miocène de Malembe (première note sur les mammifères fossiles du Congo). C. r. Congr. natn. Sci., Brux., 2nd, 1: 715-720.

DECHASEAUX, C. 1958. Sirenia. In Piveteau, J. Traité de Paléontologie. 6 (2): 333-363.

DELFORTRIE, E. 1880. Découverte d'un squelette entier de Rhytiodus dans les faluns aquitaniens. Act. Soc. linn. Bordeaux, (4) 4: 131-144.

DEPÉRET, C. & ROMAN, F. 1920. Le Halitherium serresi des sables pliocènes de Montpellier et les rameaux phyletiques des sireniens fossiles de l'ancien monde. Archs Mus. Hist. nat. Lyon, 12: 1-56.

DERANIYAGALA, P.E.P. 1969. A Miocene vertebrate faunule from the Malu member of Ceylon. Spolia zeylan., 31: 551-570.

D'ERASMO, G. 1934. Su alcuni avanzi di vertebrati terziari della Sirtica. Missione della R. Accad. d'Italia a Cufra (1931-IX), 3: 259-279.

DESIO, A. 1968. History of geologic exploration in Cyrenaica. Petrol. Explor. Soc. Libya. Annu. Field Conf., 10th: 79-113.

DESIO, A. 1971. Outlines and problems in the geomorphological evolution of Libya, from the Tertiary to the present day. In Gray, C. (Ed.). Symposium on the geology of Libya: 11-36. Tripoli.

DOMNING, D.P. 1970a. Sirenian evolution in the north Pacific and the origin of Steller's Sea Cow. Annu. Conf. biol. Sonar & Diving Mammals. 7th. Proc.: 217-220.

DOMNING, D.P. 1971. Sirenians as guide fossils in West Coast late Tertiary correlation - a prospectus. Geol. Soc. Amer., Abstr., 3: 110-111.

DOMNING, D.P. 1972. Sirenians and desmostylians in West Coast Miocene stratigraphy. In The Pacific Coast Miocene Biostratigraphic Symposium. Proc., Soc. Econ. Paleontol. Mineral., Pacific Section: 146-149.

DOUST, H. 1968. Palaeoenvironment studies in the Miocene of Libya. Ph.D. Thesis, University of London.

EDINGER, T. 1939. Two notes on the central nervous system of fossil Sirenia. Bull. Fac. Sci. Egypt. Univ., 19: 43-57.

ENNOUCHI, E. 1954. Un sirénien, Felsinotherium cf. serresi, à Dar bel Hamri. Notes Mém. Serv. Mines Carte géol. Maroc, 9: 77-82.

FERNAND, V.S.V. 1953. The teeth of the dugong. Ceylon J. Sci., 25: 139-147.

FLEISCHER, G. 1971. Über Schwingungsmessungen am Skelett des Mittelohres von Halicore (Sirenia). Z. Säugetierk., 36: 350-360.

FLOT, L. 1887. Note sur le Prohalicore dubaleni. Bull. Soc. géol. Fr., (3) 15: 11.

FLOWER, W.H. 1874. Description of the skull of a species of Halitherium (H. canhami) from the Red Crag of Suffolk. Q. Jl geol. Soc. Lond., 30: 1-7.

FREUDENTHAL, M. 1970. Fossiele zeekoeien in het Eoceen van Taulanne. Experimenteel Geologisch Onderwijs, 1969/1970: 64-65.

FREUND, L. 1950. Bibliography of the mammalian order Sirenia. Věst. čsl. zool. Spol., 14: 161-181.

FUCHS, H. 1959. Sziren - lelet Erdelyből (Ein Sirenenfund aus Siebenbürgen). Földt. Közl., 89: 326-328.

FUCHS, H. 1970. Schädelfragment einer Sirene aus dem Eozän von Cluj, SR Rumänien. Geologie, 10: 1185-1191.

GARD, L.M., LEWIS, G.E. & WHITMORE, F.C. 1972. Steller's Sea Cow in Pleistocene Interglacial beach deposits on Amchitka, Aleutian Islands. Bull. geol. Soc. Am., 83: 867-870.

GAUDRY, A. 1884. Sur un sirénien d'espèce nouvelle trouvé dans le bassin de Paris. Bull. Soc. géol. Fr., (3) 12: 372-376.

GINSBURG, L. & JANVIER, P. 1971. Les mammifères marins des faluns miocènes de la Touraine et de l'Anjou. Bull. Mus. Hist. nat., Paris, (3) 22: 161-195.

GORDON, W.A. 1961. Planktonic foraminifera and the correlation of the middle Tertiary rocks of Puerto Rico. Micropaleontology, 7: 451-460.

GRIGORESCU, D. 1967. Asupra prezentei unor fragmente scheletice de sirenide din Paleogenul de la Albești-Muscel. Anal. Univ. C. I. Parhon, 16: 73-78.

HAMILTON, W.R. 1970. The Lower Miocene ruminants of Africa. Ph.D. Thesis,

University of Bristol.

HAMILTON, W.R. 1972. The Lower Miocene ruminants of Gebel Zelten, Libya. Bull. Br. Mus. nat. Hist. (Geol.), 21: 73-150.

HARRIS, J.M. 1969. Prodeinotherium from Gebel Zelten, Libya. Ph.D. Thesis, University of Bristol.

HAY, O.P. 1922. Description of a new fossil sea cow from Florida, Metaxytherium floridanum. Proc. U. S. natn. Mus., 61: 1-4.

HEIM, A. 1919. Geologie der Schweiz. 1. xx + 704pp. Leipzig.

HEUVELMANS, B. 1941a. Notes sur la dentition des siréniens. 1: La formule dentaire du lamantin (Trichechus). Bull. Mus. r. Hist. nat. Belg., 17, 21: 1-15.

HEUVELMANS, B. 1941b. Notes sur la dentition des siréniens. 2: Morphologie de la dentition du lamantin (Trichechus). Bull. Mus. r. Hist. nat. Belg., 17, 26: 1-11.

HEUVELMANS, B. 1941c. Notes sur la dentition des siréniens. 3: La dentition du dugong. Bull. Mus. r. Hist. nat. Belg., 17, 53: 1-14.

HEUVELMANS, B. 1942. Notes sur la dentition des siréniens. 4: Le cas de Prorastoma veronense. Bull. Mus. r. Hist. nat. Belg., 18, 3: 1-6.

HEUVELMANS, B. 1943. Notes sur la dentition des siréniens. 5: Conclusions générales. Bull. Mus. r. Hist. nat. Belg., 19, 29: 1-16.

HOOYBERGHS, H.J.F. & DE MEUTER, F.J.C. 1972. Biostratigraphy and inter-regional correlation of the "Miocene" deposits of northern Belgium based on planktonic Foraminifera; the Oligocene-Miocene boundary on the southern edge of the North Sea Basin. Meded. K. vlaam. Acad., 34: 1-47.

HOUSE, M.R., DUNHAM, K.C. & WIGGLESWORTH, J.C. 1961. Geology and structure of the Maltese islands. In Bowen-Jones, H., Dewdney, J.C. & Fisher, W.B. Malta: background for development. 356pp. Newcastle upon Tyne.

KALTENMARK, J. 1943. Contribution a l'étude des siréniens actuels et fossiles. 3: Essai de phylogenie. Mammalia, 7: 14-25.

KELLOGG, R. 1925. A new fossil sirenian from Santa Barbara County, California. In Additions to the Tertiary history of the pelagic mammals on the Pacific coast of North America. Publs Carnegie Instn, 348: 57-70.

KELLOGG, R. 1966. Fossil marine mammals from the Miocene Calvert formation of Maryland and Virginia. 3: New species of extinct Miocene

Sirenia. Bull. U. S. natn. Mus., 247: 65-98.

KILMER, F.H. 1965. A Miocene dugongid from Baja California, Mexico. Bull. Sth. Calif. Acad. Sci., 63: 57-74.

KINGDON, J. 1971. East African mammals: An atlas of evolution in Africa. x + 446pp. London.

KLEINSMIEDE, W.F.J. & BERG, N.J. van den. 1968. Surface geology of the Jabal al Akhdar, northern Cyrenaica, Libya. Petrol. Explor. Soc. Libya. Annu. Field Conf., 10th: 115-123.

KLITZSCH, E. 1968. Outline of the geology of Libya. Petrol. Explor. Soc. Libya. Annu. Field Conf., 10th: 71-78.

KOCH, A. 1903. Tarnócz im Komitat Nógrád, als neuer, reicher Fundort fossiler Haifischzähne. Földt. Közl., 33: 139-164.

KOENIGSWALD, G. von. 1952. Fossil sirenians from Java. Proc. Sect. Sci. K. ned. Akad. Wet., (B), 55: 610-612.

KRETZOI, M. 1941. Sirenavus hungaricus, ein neuer Prorastomide aus dem Mitteleozän (Lutetium) von Felsögalla in Ungarn. Annls hist.-nat. Mus. natn. hung., 34: 146-156.

KRETZOI, M. 1951. Neuer Sirenen-Typus aus dem ungarischen Miozän. Földt. Közl., 81: 438-441.

KRUTZSCH, W. & LOTSCH, D. 1958. Übersicht über die paläogeographische Entwicklung des zentraleuropäischen Alttertiärs (ohne Tethys-Raum). Ber. geol. Ges. D. D. R., 3: 99-110.

LARTET, E. 1866. Note sur deux nouveaux siréniens fossiles des terrains tertiaires du bassin de la Garonne. Bull. Soc. géol. Fr., (2) 23: 673-686.

LEPSIUS, G.R. 1882. Halitherium schinzi, die fossile Sirene des Mainzer Beckens. Abh. Mittelrhein. geol. Ver., 1: 1-200.

LYDEKKER, R. 1887. Catalogue of the fossil Mammalia in the British Museum. Part 5: Containing the group Tillodontia, the orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata, and Supplement. xxxv + 345pp. London.

MAGLIO, V.J. 1970. Early Elephantidae of Africa and a tentative correlation of African Plio-Pleistocene deposits. Nature, Lond., 225: 328-332.

MAGNIER, P. 1962. Étude géologique du gisement de Vertébrés du Gebel Zelten (Libye). C. r. Séanc. Soc. géol. Fr., 2: 55-57.

MATTHEW, W.D. 1916. New sirenian from the Tertiary of Porto Rico, West Indies.

Ann. N. Y. Acad. Sci., 27: 23-29.

McDOWELL, S.B. 1958. The Greater Antillean insectivores. Bull. Am. Mus. nat. Hist., 115: 113-214.

McFADYEN, W.A. 1952. In Haas, O. & Miller, A.K. Eocene nautiloids of British Somaliland. Bull. Am. Mus. nat. Hist., 99: 313-354.

McKENZIE, K.G. 1967. The distribution of Caenozoic marine Ostracoda from the Gulf of Mexico to Australasia. In Adams, C.G. & Ager, D.V. (Eds). Aspects of Tethyan Biogeography. Publs Syst. Ass., 7: 219-238.

MOUSSA, M. & SEIGLIE, G.A. 1970. Revision of mid-Tertiary stratigraphy of southwestern Puerto Rico. Bull. Am. Assoc. Petrol. Geol., 54: 1887-1898.

MÜLLERRIED, F.K.G. 1932. Primer hallazgo de un sirenido fosil en la Republica Mexicana. An. Inst. biol. Mex., 3: 71-73.

NEWTON, E.T. 1891. The vertebrates of the Pliocene deposits of Britain. Mem. geol. Surv. U. K., 12. xi + 138pp.

OWEN, R. 1845. Odontography: or a treatise on the comparative anatomy of the teeth, etc.. lxxiv + 655pp. London.

OWEN, R. 1855. On the skull of a mammal (Prorastomus sirenoides Owen) from the island of Jamaica. Q. Jl geol. Soc. Lond., 11: 541-543.

OWEN, R. 1875a. On fossil evidences of a sirenian mammal (Eotherium aegyptiacum Owen) from the Nummulitic Eocene of the Mokattam Cliffs, near Cairo. Q. Jl geol. Soc. Lond., 31: 100-105.

OWEN, R. 1875b. On Prorastomus sirenoides Owen. Q. Jl geol. Soc. Lond., 31: 559-567.

PASCUAL, R. 1953. Sobre nuevos restos de sirenidos del Mesopotámiense. Revta Assoc. geol. argent., 8: 163-181.

PASCUAL, R. 1966. Datos preliminares sobre el primer resto de un sirenio (Dugongidae) del Mioceno superior ("Paranaense") de la Argentina (abstract). Ameghiniana, 4: 242

PATTE, E. 1962. Présence de l'Halitherium dans l'Oligocene du Poitou. Bull. Soc. géol. Fr., (7) 4: 536-537.

PAULA COUTO, C. de. 1967. Contribuição à paleontologia do Estado do Pará. Um sirênio na Formação Pirabas. In Simpósio sôbre a biota amazônica. Atas, 1: 345-357.

PETIT, G. 1928. Les vertèbres cervicales des siréniens actuels. Archs Mus. natn. Hist. nat., Paris, (6) 3: 243-299.

PETIT, G. 1955. Ordre des Siréniens. In Grassé, P.-P. Traité de Zoologie. 17 (1): 918-1001. Paris.

PIAZ, G. dal. 1937. Halitherium sp.. Memorie Ist. geol. miner. Univ. Padova, 11: 1-5.

PIETERSZ, C.R. 1968. Proposed nomenclature for rock units in northern Cyrenaica. Petrol. Explor. Soc. Libya. Annu. Field Conf., 10th: 125-130.

PRATER, S.H. 1928. Dugong or sea cow (Halicore dugong). J. Bombay nat. Hist. Soc., 33: 84-99.

REINHART, R.H. 1951. New genus of sea cow from the Miocene of Colombia. Univ. Calif. Publs geol. Sci., 28: 203-214.

REINHART, R.H. 1953. Diagnosis of the new mammalian order Desmostylia. J. Geol., 61: 187.

REINHART, R.H. 1959. A review of the Sirenia and Desmostylia. Univ. Calif. Publs geol. Sci., 36: 1-146.

RICHARD, M. 1946. Les gisements de mammifères tertiaires d'Aquitaine. Mém. Soc. géol. Fr., 52: 380pp.

ROBINEAU, D. 1969. Morphologie externe du complexe osseux temporal chez les siréniens. Mém. Mus. natn. Hist. nat., Paris. (A), 60: 1-32.

RUSSELL, D.E. 1964. Les mammifères paléocènes d'Europe. Mém. Mus. natn. Hist. nat., Paris. (C), 13: 1-324.

RUSSELL, D.E. & SIGOGNEAU, D. 1965. Étude de moulages endocraniens de mammifères paléocènes. Mém. Mus. natn. Hist. nat., Paris. (C), 16: 1-34.

SAID, R. & MARTIN, L. 1964. Cairo area geological excursion notes. Petrol. Explor. Soc. Libya. Annu. Field Conf., 6th: 107-121.

SAVAGE, R.J.G. 1967. Early Miocene mammal faunas of the Tethyan region. In Adams, C.G. & Ager, D.V. (Eds). Aspects of Tethyan Biogeography. Publs Syst. Ass., 7: 247-282.

SAVAGE, R.J.G. 1968. In Selley, R.C. Near-shore marine and continental sediments of the Sirte basin, Libya. Proc. geol. Soc. Lond., 1648: 85-88.

SAVAGE, R.J.G. 1969. Early Tertiary mammal locality in southern Libya. Proc. geol. Soc. Lond., 1657: 167-171.

SAVAGE, R.J.G. 1971. Review of the fossil mammals of Libya. In Gray, C. (Ed.). Symposium on the geology of Libya: 215-225. Tripoli.

SAVAGE, R.J.G. & HAMILTON, W.R. 1973. Introduction to the Miocene mammal faunas of Gebel Zelten, Libya. Bull. Br. Mus. nat. Hist. (Geol.), 22: 513-527.

SAVAGE, R.J.G. & WHITE, M.E. 1965. Two mammal faunas from the early Tertiary of central Libya. Proc. geol. Soc. Lond., 1623: 89-91.

SCHUCHERT, C. 1955. Atlas of paleogeographic maps of North America. ix + 177pp. New York.

SCULTHORPE, C.D. 1967. The biology of aquatic vascular plants. xviii + 610pp. London.

SELLEY, R.C. 1966. The Miocene rocks of the Marada and Jebel Zelten area, central Libya: A study of shoreline sedimentation. Petrol. Explor. Soc. Libya. Guidebook. iii + 30pp. Tripoli.

SELLEY, R.C. 1967. Palaeocurrents and sediment transport in nearshore sediments of the Sirte basin, Libya. J. Geol., 75: 215-223.

SELLEY, R.C. 1968. Near-shore marine and continental sediments of the Sirte basin, Libya. Proc. geol. Soc. Lond., 1648: 81-90.

SELLEY, R.C. 1969. Near-shore marine and continental sediments of the Sirte basin, Libya. Q. Jl geol. Soc. Lond., 124: 419-460.

SELLEY, R.C. 1971. Structural control of Miocene sedimentation in the Sirte Basin. In Gray, C. (Ed.). Symposium on the geology of Libya: 99-106. Tripoli.

SHIKAMA, T. & DOMNING, D.P. 1970. Pliocene Sirenia in Japan. Trans. Proc. palaeont. Soc. Japan, 80: 390-396.

SICKENBERG, O. 1928. Eine Sirene aus dem Leithakalk des Burgenlandes. Denkschr. Akad. Wiss., Wien, 101: 293-323.

SICKENBERG, O. 1934. Beiträge zur Kenntnis tertiärer Sirenen. 1: Die eozänen Sirenen des Mittelmeergebietes. 2: Die Sirenen des belgischen Tertiärs. Mém. Mus. r. Hist. nat. Belg., 63. 352pp.

SIEGFRIED, P. 1965. Anomotherium langewiesche n.g. n.sp. (Sirenia) aus dem Ober-Oligozän des Dobergs bei Bünde/Westfalen. Palaeontographica. (A), 124: 116-150.

SILER, W.L. 1964. A Middle Eocene sirenian in Alabama. J. Paleont., 38: 1108-1109.

SIMPSON, G.G. 1932. Fossil Sirenia of Florida and the evolution of the

Sirenia. Bull. Am. Mus. nat. Hist., 59: 419-503.

SIMPSON, G.G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. nat. Hist., 85. xvi + 350pp.

SPILLMANN, F. 1959. Die Sirenen aus dem Oligozän des Linzer Beckens (Oberösterreich) mit Ausführungen über "Osteosklerose" und "Pachyostose". Denkschr. Öst. Akad. Wiss., 110: 1-68.

THENIUS, E. 1959. Handbuch der stratigraphischen Geologie. Tertiär, 2. xi + 328pp. Stuttgart.

THENIUS, E. 1960. Wirbeltierfunde aus der paläogenen Molasse Österreichs und ihre stratigraphische Bedeutung. Verh. geol. Bundesanst., Wien, 1960: 82-88.

TOURNOUËR, [J.-] R. 1866. Sur les terrains tertiaires du bassin de la Garonne où ont été trouvés les siréniens fossiles décrits par M. Éd. Lartet. Bull. Soc. géol. Fr., (2) 23: 760-761.

TROUGHTON, E. 1941. The furred animals of Australia. xxvii + 374pp. Sydney.

TULOGDY, J. 1944. Szirénafog a Bácsi-torok eocén felső durvamészkövéből. Revta Múz. geol.-miner. Univ. Cluj, 2:

VAN COUVERING, J.A. 1972. Radiometric calibration of the European Neogene. In Bishop, W.W. & Miller, J.A. (Eds). Calibration of hominoid evolution: 247-271. Edinburgh.

VAN COUVERING, J.A. & MILLER, J.A. 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. Nature, Lond., 221: 628-632.

VAN VALEN, L. 1971. Adaptive zones and the orders of mammals. Evolution, Lancaster, Pa., 25: 420-428.

WERNER, J. 1970. Beschrijving Nummulieten van de zeekoei envindplaats Taulanne. Experimenteel Geologisch Onderwijs, 1969/1970: 65-66.

WESTERMANN, G.E.G. (Ed.). 1969. Sexual dimorphism in fossil metazoa and taxonomic implications. iv + 251pp. Stuttgart.

WIGHT, A. 1971. Palaeogene vertebrates from Libya. 1: The geology of the Eocene-Oligocene sediments at Dor el Talha, southern Libya, with special reference to the vertebrate fauna. 2: The Proboscidea (excluding Barytherium) from Dor el Talha, southern Libya; and a study of the genus Moeritherium. Ph.D. Thesis, University of Bristol.

WILHELM, W. 1962. Eine versteinerte Seekuh aus dem Alzeyer Meeressand. Natur

Mus., Frankf., 92: 51-53.

WILKINSON, A. 1972. The Lower Miocene Suidae of Africa. Ph.D. Thesis, University of Bristol.

WILLS, L.J. 1951. A palaeogeographical atlas of the British Isles and adjacent parts of Europe. 64pp. London.

WOODWARD, H. 1885. On the fossil Sirenia in the British Museum. Geol. Mag., 2: 412-425.

ZBYSZEWSKI, G. 1944. Note sur la découverte d'un humérus de Metaxytherium petersi Abel dans l'Helvétien de Lisbonne. Bolm Soc. geol. Port., 4: 69-72.

ZBYSZEWSKI, G. 1949. Les Vertébrés du Burdigalien supérieur de Lisbonne. Serv. géol. Port., 1949: 77pp.

ZDANSKY, O. 1938. Eotherium majus sp.n., ein neue Sirene aus dem Mitteleozän von Agypten. Palaeobiologica, 6: 429-434.

ZIGNO, A. de. 1875. Sirenii fossili trovato del Veneto. Mem. R. Ist. veneto Sci., 18: 427-456.

APPENDIX A

MEASUREMENTS

TABLE I

Skull and mandible measurements of Prorastomus sirenoides (A), Libysiren sickenbergi (B'), Protosiren fraasi (B"), Eotheroides aegyptiacum (C'), Eotheroides cf. E. aegyptiacum (C"), and Eotheroides libycum (C"').

The inclusion of the measurements of four species in addition to Libysiren sickenbergi is necessary because none of the previous workers on Eocene sirenians has published tables of comparative measurements.

Key to the measurements

Premaxillae

1. Sagittal length of premaxillae
2. Maximum width of premaxillae
3. Sagittal length of symphysis
4. Maximum width across symphysis
5. Maximum height of symphysis
6. Sagittal length of mesorostral fossa
7. Maximum width of mesorostral fossa

Maxillae

8. Sagittal length of maxillae
9. Maximum length of maxillae
10. Maximum width of maxillae

Nasals

11. Sagittal length of nasals
12. Maximum length of nasals
13. Maximum width of nasals

Frontals

14. Sagittal length of frontals
15. Maximum length of frontals
16. Supraorbital width of frontals

Parietals

17. Sagittal length of parietals
18. Maximum length of parietals
19. Maximum anterior width of parietals
20. Maximum posterior width of parietals
21. Minimum width of parietals

Frontals + Parietals

22. Sagittal length of frontals + parietals

Occipital

23. Height of occipital
24. Maximum width of occipital
25. Maximum width across occipital condyles
26. Distance between tips of pareoccipital processes
27. Width of foramen magnum
28. Height of foramen magnum

Squamosal

29. Maximum width across zygomatic processes

Sphenoid

30. Distance between tips of pterygoid processes

Vomer

31. Sagittal length of vomer

Petrotympanic

32. Length of tegmen tympani
33. Distance from anterior end of pars petrosa to posterior end of pars mastoidea
34. Distance between attachment points of tympanic ring

Mandible

35. Length of mandible
36. Maximum width of mandible
37. Sagittal length of symphysis
38. Maximum width across symphysis
39. Maximum height of symphysis
40. Distance between ventral edge of angular process and dorsal surface of condyle

(ALL MEASUREMENTS IN MILLIMETRES)

TABLE I

		A	B′		B″	
		BM(NH) 44897	BM(NH) M19100a	UB 20607/20608[1]	SMF M3742	SMF M3743
PREMAXILLAE						
	1.	98	143	171[1]+		
	2.	c. 50	102	c.102[1]		
	3.	38	42+	73[1]		
	4.	44	83	82[1]		
	5.	52	32+	56[1]		
	6.	c. 55	82			
	7.	30	70			
MAXILLAE						
	8.		91+			
	9.		179			
	10.		174			
NASALS						
	11.	c. 40	47			
	12.	c. 43	70	76		
	13.	c. 46	79			
FRONTALS						
	14.		55	59	c 50	
	15.		117	130		
	16.	c. 90	c.185	c.184		
PARIETALS						
	17.		c.130	c.140	64	79
	18.		c.150	c.170		
	19.		89	86	56	c. 58
	20.		c.116	c.112	74+	80
	21.		76	75	48	59
FRONTALS + PARIETALS						
	22.	126	c.185	c.199	c.114	

TABLE I (cont.)

		A	B′		B″	
OCCIPITAL						
	23.	48+	118			
	24.		166			
	25.		110			
	26.		132			
	27.	23	57			
	28.	21	45			
SQUAMOSAL						
	29.	150+	232			
SPHENOID						
	30.		66			
VOMER						
	31			60[1]		
PETROTYMPANIC						
	32.		55			
	33.	c. 27	64			
	34.	c. 12	24			

TABLE I (cont.)

		C′	C″				C‴		
		BSM 1905 XIII e1	GIA Hs 71-19	RGM St. 177774	RGM St. 177775	GIA Hs 69-5	BM(NH) M10910	MNHN 1913-22	BSM 1902 XI 61
PREMAXILLAE									
	1.		132+				160+	176	
	2.		c. 73				77	77	
	3.		59+				97+	94	104+
	4.		44				53	49	54
	5.		76				104	60	
	6.				77		91	c.76	
	7.		c. 47				41	41	
MAXILLAE									
	8.		85+						
	9.		143+						
	10.		c.144	106+			143		
NASALS									
	11.				c. 18		8	9	
	12.				c. 40		34	39	
	13.		c. 66		c. 54		59	59	58
FRONTALS									
	14.			61+			94	80	c. 82
	15.			c. 99			115	93	
	16.		c.130	c. 98	107+		104	108	117+
PARIETALS									
	17.	c. 69	c. 66	61			70	96	c. 81
	18.						119	123	c.108
	19.		c. 44				56	53	
	20.	c. 52	c. 53	54			72		c. 54
	21.	c. 34	c. 44	41			48	49	
FRONTALS + PARIETALS									
	22.			122+			c.164	176	c.163

TABLE I (cont.)

		C'	C''			C'''	
OCCIPITAL							
	23.	74					
	24.	82				55+	
	25.	62					
	26.	c. 56					
	27.	28					
	28.	20					
SQUAMOSAL							
	29.			c.160	c.148	168	c.167
SPHENOID							
	30.	46+	c. 85		89-	c. 80	
VOMER							
	31.						
PETROTYMPANIC							
	32.						
	33.			c. 42	c. 48		
	34.				c. 20		

		C'' GIA Sm71-101	C''' MNHN 1913-22
MANDIBLE			
	35.	272+	191
	36.		170+
	37.	c.60	65
	38.		65
	39.	c. 74	64
	40.	c.140	

TABLE II

Tooth measurements of Eotheroides cf. E. aegyptiacum

		RGM St. 177774		RGM St. 177775		GIA Hs 71-19		GIA Sm71-101		GIA Sm71-102	GIA Hs 69-3		GIA Hs 69-4	
		l.	r.	l.	r.	l.	r.	l.	r.	r.	l.	r.	l.	r.
M^1	L	c. 15.0												
	W	c. 16.6												
M^2	L	c. 15.9			c. 17.1	c. 17.1	c. 17.5	c. 17.3						
	W				c. 18.6	c. 19.5	c. 19.0	c. 19.7						
M^3	L				c. 22.2	c. 20.7	c. 20.5	c. 22.6		c. 24.2				
	W				c. 16.7	c. 18.9	c. 18.8	c. 19.3	c. 19.6	c. 19.4				
M_2	L							c. 21.6			c. 20.1			
	W							c. 15.6						c. 17.5
M_3	L							c. 25.7	c. 27.2					c. 26.0
	W							c. 16.2	c. 15.8					c. 19.3

TABLE III

Skull and mandible measurements of Rytiodus capgrandi (A') (from Delfortrie, 1880) and Rytiodus zeltenensis (A").

Some of Delfortrie's measurements for R. capgrandi are not given because they are exaggerated by his use of a distorted specimen.

Key to the measurements

Premaxillae

1. Maximum width of premaxillae
2. Maximum width across symphysis
3. Sagittal length of mesorostral fossa
4. Maximum width of mesorostral fossa

Maxillae

5. Maximum width of maxillae

Nasals

6. Maximum length of nasals
7. Maximum width of nasals
8. Anterior width of each nasal

Frontals

9. Maximum length of frontals
10. Supraorbital width of frontals

Parietals

11. Sagittal length of parietals
12. Maximum length of parietals

Squamosal

13. Maximum width across zygomatic processes

Sphenoid

14. Distance between tips of pterygoid processes

Jugal

15. Maximum width across zygomatic processes

(ALL MEASUREMENTS IN MILLIMETRES)

TABLE III

		A'	A''	
		I	BM(NH) M19101a	UB 20853a
PREMAXILLAE				
	1.		c.172	182
	2.			c.139
	3.		c.195	
	4.	60	89	92
MAXILLAE				
	5.		c.235	c.244
NASALS				
	6.			91
	7.		c.109	135
	8.			42
FRONTALS				
	9.		c.133	
	10.	240		c.246
PARIETALS				
	11.		c. 94	
	12.		c.154	
SQUAMOSAL				
	13.		c.234	
SPHENOID				
	14.		c. 85	
JUGAL				
	15.	300		c.327

APPENDIX B

KEYS TO THE SIRENIAN FAMILIES, SUBFAMILIES, AND GENERA

KEY TO THE FAMILIES AND SUBFAMILIES

1. Periotic attached to skull wall.....Prorastomidae
   Periotic not attached to skull wall.....2

2. Complete eutherian dentition.....3
   Modified eutherian dentition.....4

3. Lacrimal duct absent; alisphenoid canal present.....Protosirenidae
   Lacrimal duct present; alisphenoid canal absent.....Eotheroididae

4. Numerically increased dentition; six cervicals.....Trichechidae
   Numerically reduced dentition; seven cervicals.....Dugongidae 5

5. M^3 unreduced.....6
   M^3 reduced or absent.....9

6. Incisor tusks markedly flattened.....Rytiodinae
   Incisor tusks cylindrical.....7

7. Nasals join in mid-line.....Halitheriinae
   Nasals separated by frontals in mid-line or absent.....8

8. Cheek teeth retain enamel after erupting.....Metaxytheriinae
   Cheek teeth lose enamel after erupting.....Dugonginae

9. M^3 reduced to a flattened button.....Miosireninae
   M^3, and all other teeth, absent.....Hydrodamalinae

The arrangement of the sirenian families and subfamilies in this key does not reflect the actual phylogeny that is laid out in Chapter 4.

KEY TO THE GENERA

1. Periotic attached to skull wall.....*Prorastomus*
   Periotic not attached to skull wall.....2

2. Complete eutherian dentition.....3
   Modified eutherian dentition.....6

3. Lacrimal duct absent; alisphenoid canal present.....4
   Lacrimal duct present; alisphenoid canal absent.....5

4. Large genus; post-tympanic process present.....*Libysiren*
   Small genus; post-tympanic process absent.....*Protosiren*

5. Skull not dolicocephalic; $M^3 < M^2$; humerus short and fat...*Eotheroides*
   Skull dolicocephalic; $M^3 > M^2$; humerus long and thin.....*Prototherium*

6. Numerically increased dentition; six cervicals.....7
   Numerically reduced dentition; seven cervicals.....8

7. Hypocone forming right-angled crest with cingulum.....*Sirenotherium*
   Hypocone not attached to cingulum.....*Trichechus*

8. M^3 unreduced.....9
   M^3 reduced or absent.....15

9. Nasals join in mid-line.....10
   Nasals separated by frontals in mid-line.....12

10. Four premolars in upper jaw.....*Halitherium*
    Two premolars in upper jaw.....11

11. Long nasals.....*Anomotherium*
    Short nasals.....*Thalattosiren*

12. Incisor tusks absent.....*Caribosiren*
    Incisor tusks present (at least in male).....13

13. Incisor tusks markedly flattened.....*Rytiodus*
    Incisor tusks cylindrical.....14

14. Miocene genus.....*Metaxytherium*
    Pliocene genus.....*Felsinotherium*

15. M^3, and all other teeth, absent.....*Hydrodamalis*
    M^3 reduced.....16

16. M^3 enamelled, but reduced to a flattened button.....*Miosiren*
    M^3 without enamel and with open roots.....*Dugong*

The arrangement of the sirenian genera in this key does not reflect the actual phylogeny that is laid out in Chapter 4.

APPENDIX C

SIRENIAN DISTRIBUTION MAPS

MAPS

Figure I World:

Recent sirenian distribution

Figures IIa-e Tethys:

IIa Eocene sirenian distribution

IIb Oligocene sirenian distribution

IIc Lower Miocene sirenian distribution

IId Middle-Upper Miocene sirenian distribution (includes Langhian and Helvetian sites)

IIe Pliocene sirenian distribution

Figures IIIa-b North America:

IIIa Palaeogene sirenian distribution

IIIb Neogene sirenian distribution

Figure IV South America:

Cenozoic sirenian distribution

Figure V Indo-Pacific:

Cenozoic sirenian distribution

NOTE The sources listed in the keys to Figures II-V are not necessarily the original descriptions, but also include references that are either more easily accessible or later reviews of certain taxa.

KEY TO FIGURE I

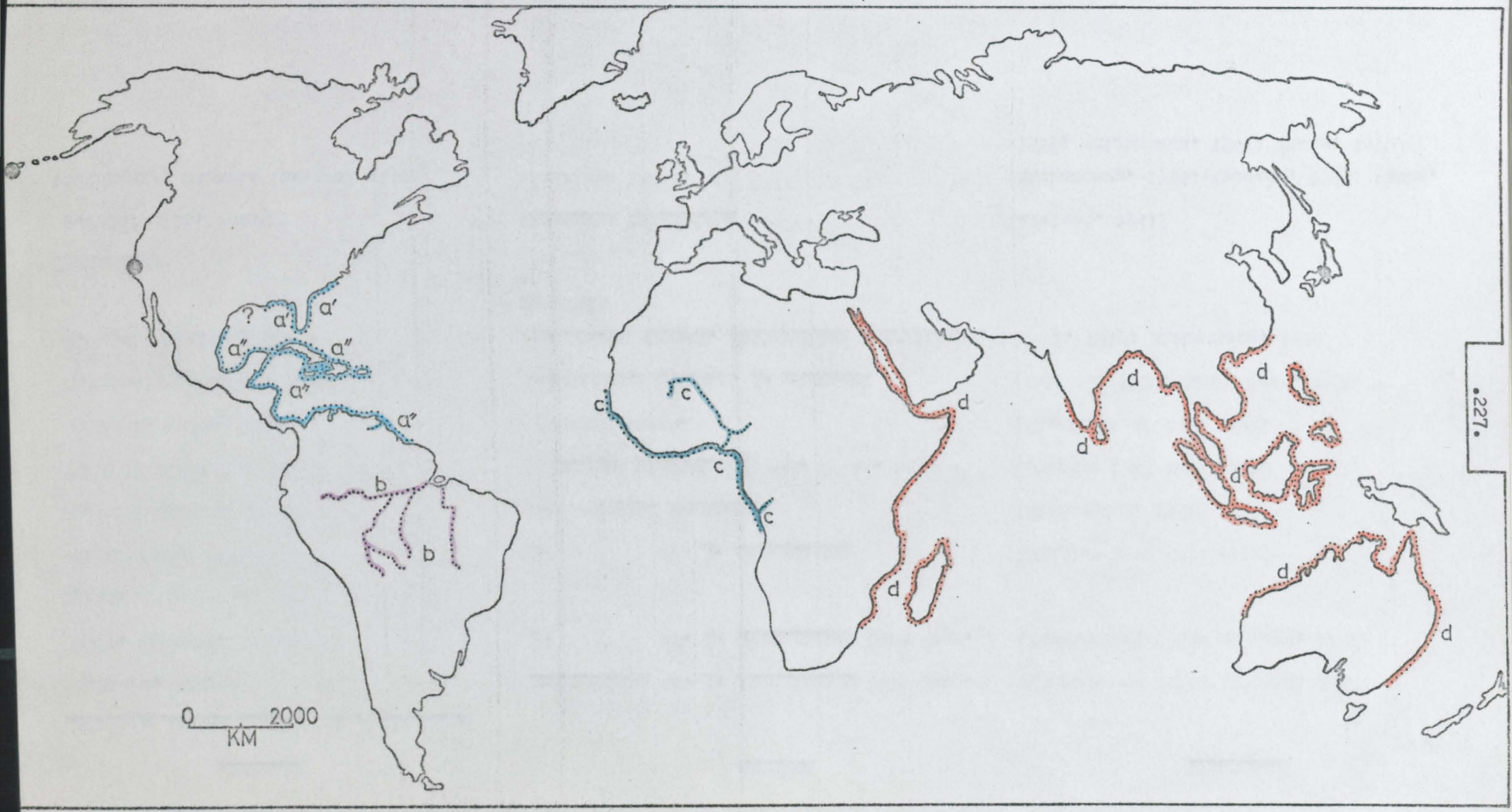
Trichechidae

a' *Trichechus manatus latirostris*
a" *T. M. manatus*
b *T. inunguis*
c *T. senegalensis*

Dugongidae

d *Dugong dugon*
● *Hydrodamalis* spp.

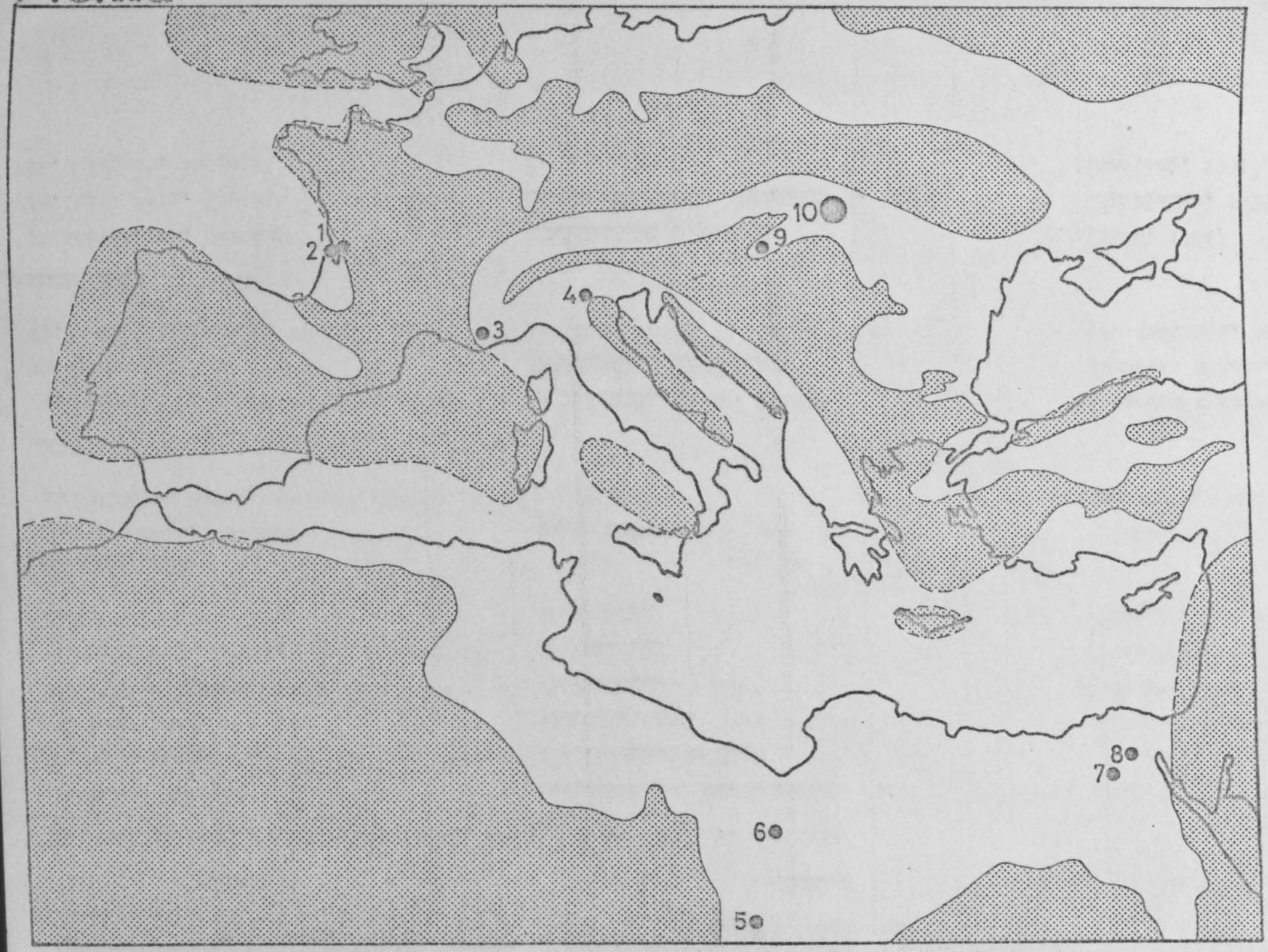
FIG. I



KEY TO FIGURE IIa

Locality	Species	Source(s)
Atlantic Basins (Aquitaine Basin etc.)		
1. Blaye, France	Eotheroides cf. E. aegyptiacum (see Chap.2)	(Sickenberg, 1934; Richard, 1946)
2. St. Estèphe, France	E. cf. E. aegyptiacum (see Chap.2)	(Sickenberg, 1934; Richard, 1946)
Tethys		
3. Taulanne, France	E. cf. E. aegyptiacum	(Chapter 2 of this work)
4. Monte Zuello, Italy	Prototherium veronense	(Sickenberg, 1934)
5. Bu el Haderait, Libya	Libysiren sickenbergi gen. et sp. nov.	(Chapter 1 of this work)
6. Dor el Talha, Libya	sirenian indet.	(Chapter 1 of this work)
7. Fayum Depression, Egypt	Eotheroides libycum, E. stromeri	(Andrews, 1906; Sickenberg, 1934)
8. Gebel Mokattam, Egypt	Protosiren fraasi, Eotheroides aegyptiacum, E. abeli	(Abel, 1913; Sickenberg, 1934)
Paratethys		
9. Felsögalla, Hungary	Sirenavus hungaricus	(Kretzoi, 1941)
10. Hungary; Romania (several sites)	sirenians indet.	(Sickenberg, 1934; Tulogdy, 1944; Fuchs, 1959; Grigorescu, 1967; Fuchs, 1970)

FIG. IIa



TETHYS
EOCENE

land

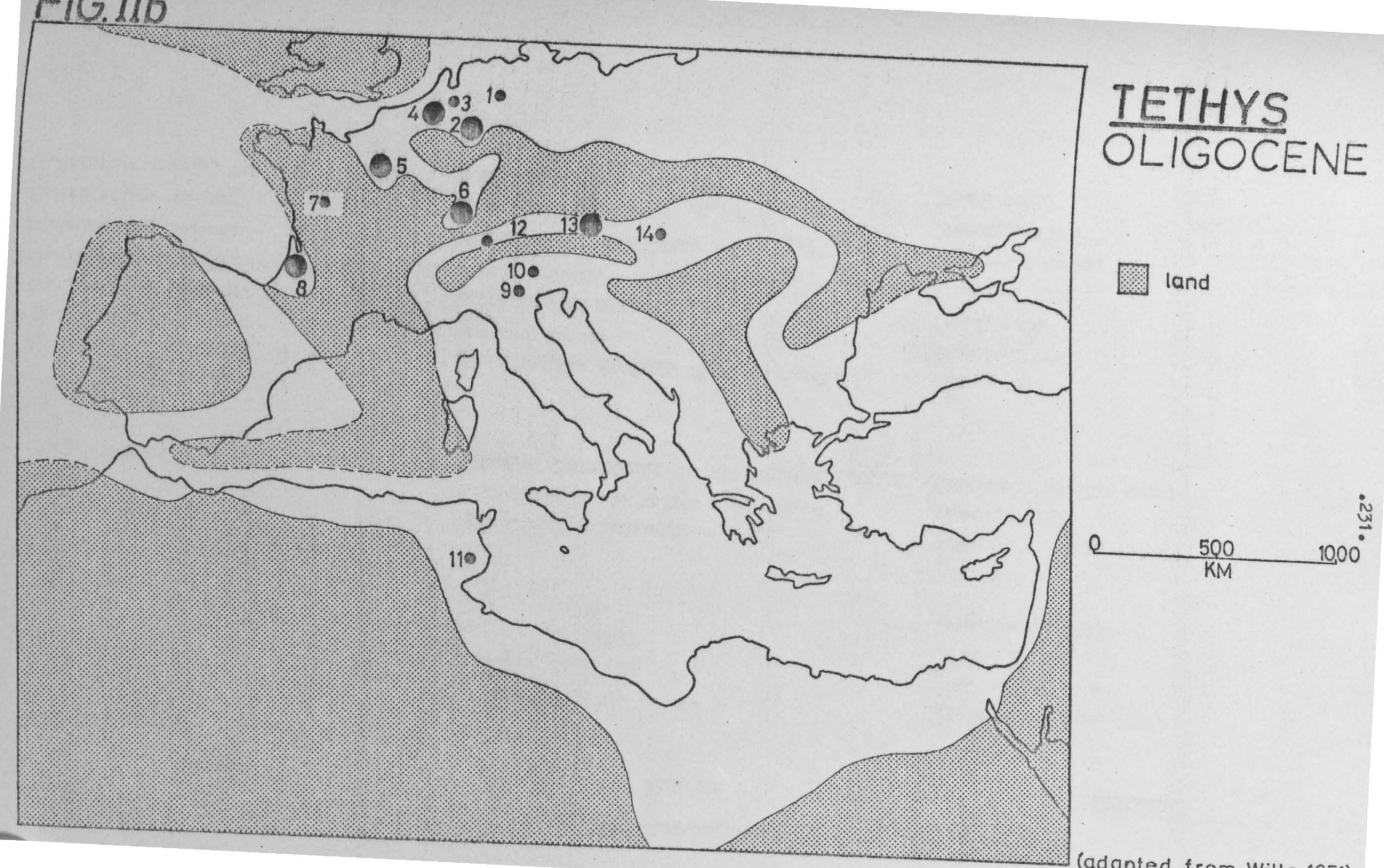
0 500 1000
KM

(adapted from Krutzsch & Lotsch, 1958)

KEY TO FIGURE IIb

Locality	Species	Source(s)
N. European Basins (North Sea Basin, Mainz Basin, Paris Basin, etc.)		
1.Bünde, Germany	*Anomotherium langewieschi*	(Siegfried, 1965)
2.Mainz Basin, Germany (several sites)	*Halitherium schinzi*	(Lepsius, 1882; Wilhelm, 1962)
3.Boom, Belgium	*Miosiren kocki* (see Chap.4)	(Sickenberg, 1934)
4.Belgium (several sites)	*H. schinzi*	(Sickenberg, 1934)
5.Paris Basin, France (several sites)	*H. schinzi*	(Gaudry, 1884; Depéret & Roman, 1920)
6.Switzerland (several sites)	*H. schinzi*	(Heim, 1919)
Atlantic Basins		
7.St. Georges, France	*Halitherium* sp. indet.	(Patte, 1962)
8.Aquitaine Basin, France (several sites)	*H. schinzi*	(Richard, 1946)
Tethys		
9.Monteviale, Castelgomberto, Italy	*H. schinzi*, *H.* sp. indet.	(Depéret & Roman, 1920)
10.Belluno, Italy	*Halitherium bellunense*	(Depéret & Roman, 1920)
11.Djebel Cherichira, Tunisia	sirenian indet.	(P. Robinson, pers. comm.)
Paratethys		
12.Tuttlingen, Germany	*Halitherium christoli*	(Abel, 1904)
13.Linz, Perg, Austria (several sites)	*H. christoli*, *H. pergense*, *H. abeli*	(Spillmann, 1959)
14.Budapest, Hungary	*H. schinzi*	(Kretzoi, 1941)

FIG. IIb

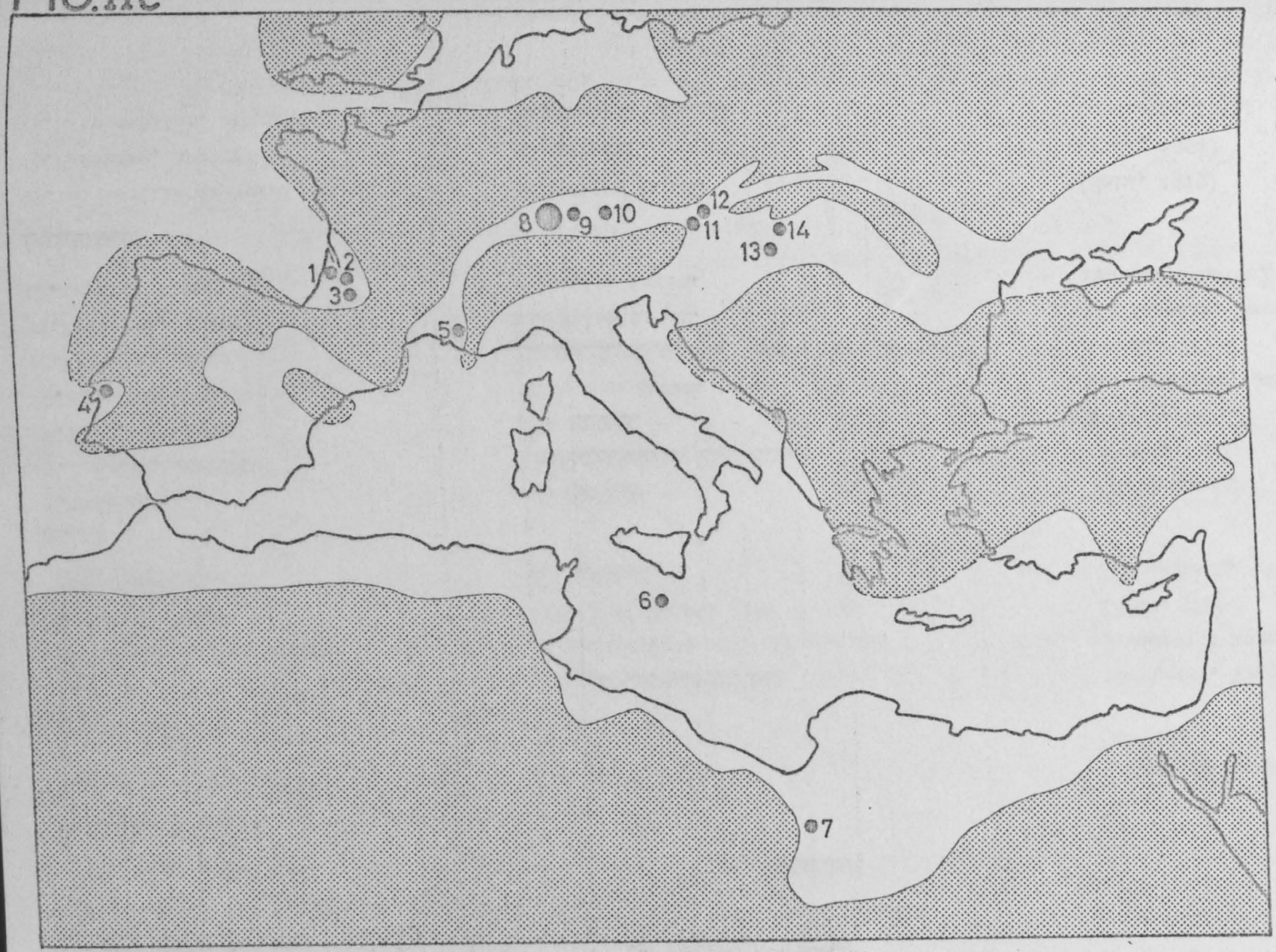


(adapted from Wills 1951)

KEY TO FIGURE IIc

Locality	Species	Source(s)
Atlantic Basins		
1.Léognan, France	Metaxytherium sp. indet.	(Depéret & Roman, 1920)
2.St. Morillon, France	Rytiodus capgrandi	(Delfortrie, 1880)
3.Sos, France	R. capgrandi	(Lartet, 1866)
4.Lisbon, Portugal	dugongid indet.	(Zbyszewski, 1949)
Tethys		
5.Beaucaire, France	Metaxytherium beaumonti	(Depéret & Roman, 1920)
6.Malta	Metaxytherium sp. indet. (see Chap.4)	(Adams, 1879)
7.Gebel Zelten, Libya	Rytiodus zeltenensis sp. nov., Metaxytherium sp. indet.	(Chapter 1 of this work)
Paratethys		
8.Switzerland (several sites)	Metaxytherium studeri, sirenian indet.	(Heim, 1919)
9.Baltringen, Germany	sirenian indet.	(Lepsius, 1882)
10.Molasse de Baviere, Germany	Metaxytherium meyeri	(Abel, 1904)
11.Obritzberg, Austria	sirenian indet.	(Thenius, 1960)
12.Eggenburg, Austria	Metaxytherium krahuletzi	(Depéret & Roman, 1920)
13.Márcfalva, Hungary	Thalattosiren petersi	(Thenius, 1959)
14.Felsőesztergály, Hungary	Halitherium cf. H. schinzi	(Koch, 1903)

FIG.IIc



TETHYS
L. MIOCENE

land

0 500 1000
KM

(adapted from Cicha, 1970)

KEY TO FIGURE IId

Locality	Species	Source(s)
N. European Basins		
1.Bergen, Holland	sirenian indet.	(author's notes)
Atlantic Basins		
2.Loire Basin, France (several sites)	Metaxytherium medium	(Cottreau, 1928; Ginsburg & Janvier, 1971)
3.Mont-de-Marsan, France	Thalattosiren aff. T. petersi	(Depéret & Roman, 1920)
4.Audon, France	dugongid indet. (see Chap.4)	(Flot, 1886)
5.Lisbon, Portugal	T. petersi	(Zbyszewski, 1944)
Tethys		
6.Mallorca	M. medium	(Thenius, 1959)
7.Sassari, Sardinia	Metaxytherium lovisatoi	(Caria, 1957)
8.Bosa, Sardinia	M. medium	(Caria, 1957)
9.Bled Douarah, Tunisia	sirenian indet.	(P. Robinson, pers. comm.)
10.Malta and Gozo	Metaxytherium sp. indet. (see Chap.4)	(Adams, 1879)
11.Provarma, Crete	sirenian indet.	(P. Sondaar, pers. comm.)
12.Sarköy, Turkey	sirenian indet.	(author's notes)
Paratethys		
13.Switzerland (several sites)	sirenians indet.	(Heim, 1919)
14.Hainburg, Austria	T. petersi	(Abel, 1904)
15.Matraszőllős, Hungary	Haplosiren lecanyi	(Kretzoi, 1951)

FIG. IId

TETHYS

M-U. MIOCENE

land

0 500 1000
KM

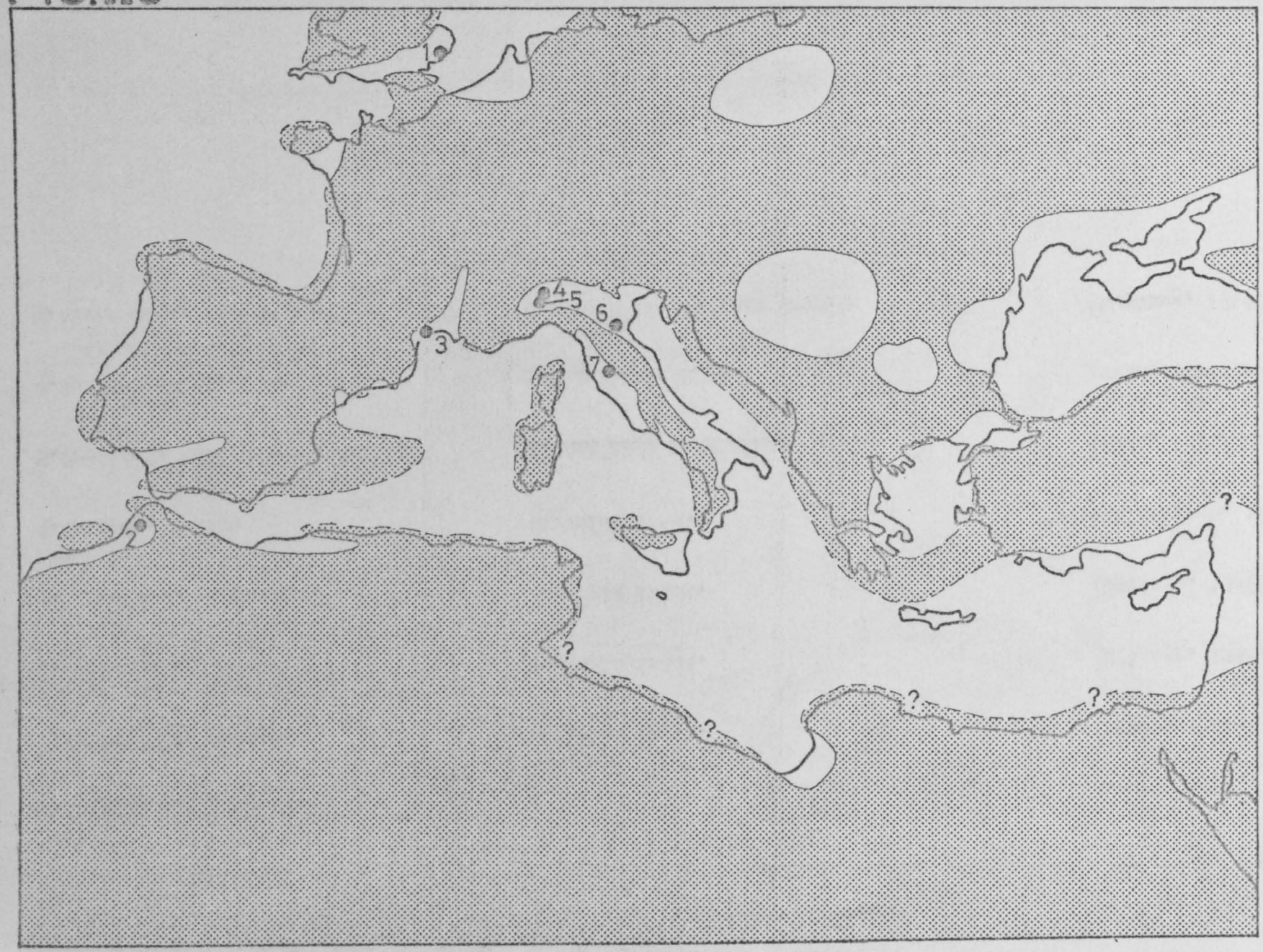
•235•

(adapted from Wills, 1951, & Cicha, 1970)

KEY TO FIGURE IIe

Locality	Species	Source(s)
N. European Basins		
1.Woodbridge, England	*Miosiren kocki*, metaxytheriine indet. (both remanié; see Chap.4)	(Flower, 1874; Newton, 1891)
Atlantic Basins		
2.Dar bel Hamri, Morocco	*Felsinotherium* cf. *F. serresi*	(Ennouchi, 1954)
Tethys		
3.Montpellier, France	*Felsinotherium serresi*	(Depéret & Roman, 1920)
4.Montiglio, Italy	*Felsinotherium forestii*	(Depéret & Roman, 1920)
5.Piemonte, Italy	*F. forestii*	(Depéret & Roman, 1920)
6.Bologna, Italy	*F. forestii*	(Depéret & Roman, 1920)
7.Siena, Italy	*F. forestii*	(Depéret & Roman, 1920)

FIG.IIe



TETHYS
PLIOCENE

land

0 500 1000
KM

•237•

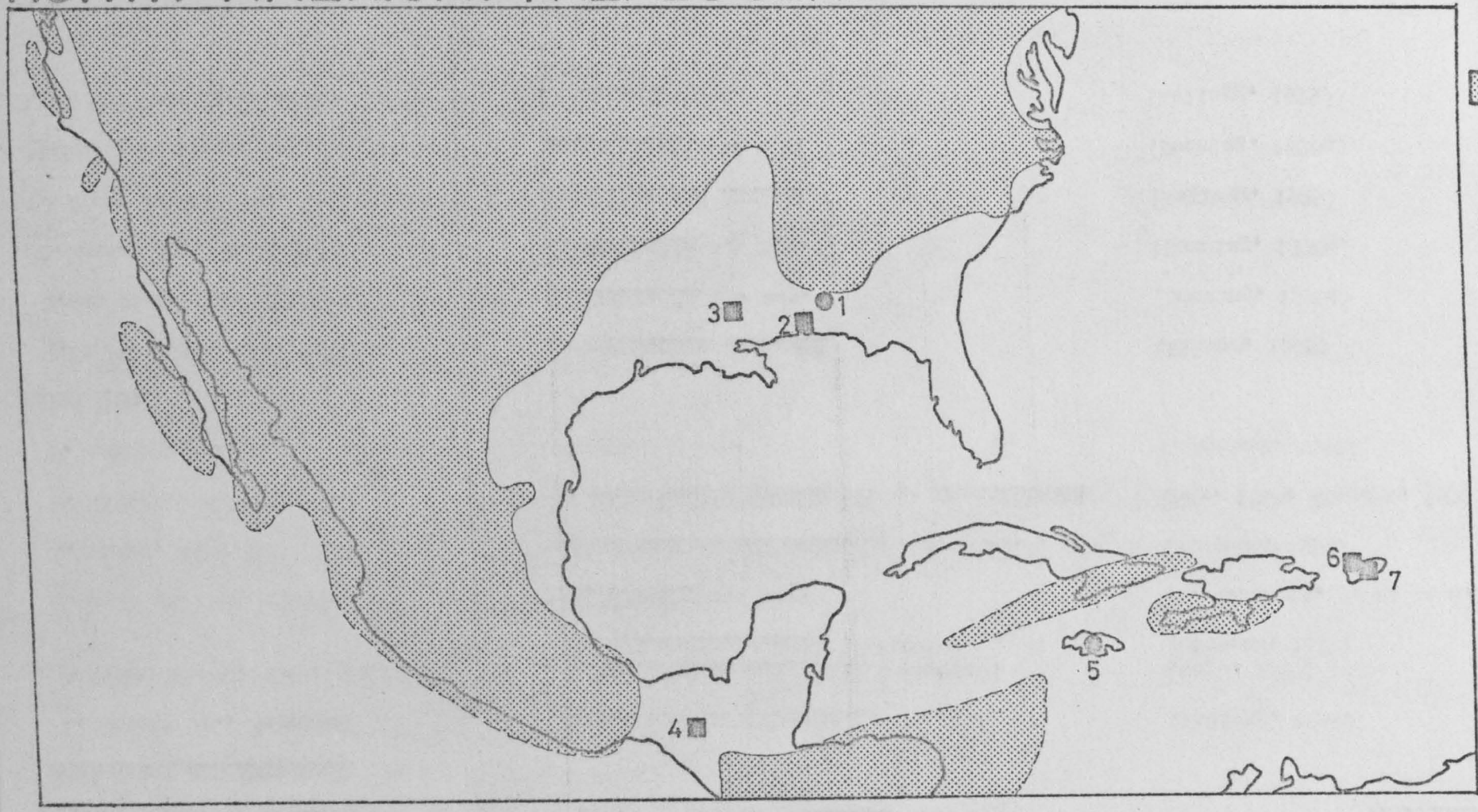
(adapted from Wills, 1951)

KEY TO FIGURE IIIa

Locality	Species	Source(s)
East Coast and Caribbean		
1.Monroe Co., Alabama	sirenian indet.	(Siler, 1964)
2.Clarke Co., Alabama	dugongid indet.	(Kellogg, 1966)
3.Wayne Co., Mississippi	dugongid indet.	(Kellogg, 1966)
4.Chiapas, Mexico	sirenian indet.	(Müllerried, 1932)
5.Freeman's Hall Estate, Jamaica	*Prorastomus sirenoides*	(Owen, 1875)
6.San Sebastian, Puerto Rico	*Caribosiren turneri*	(Reinhart, 1959)
7.Juana Diaz, Puerto Rico	dugongid indet. (see Chap.4)	(Matthew, 1916)

FIG.IIIa

NORTH AMERICA: PALAEOGENE



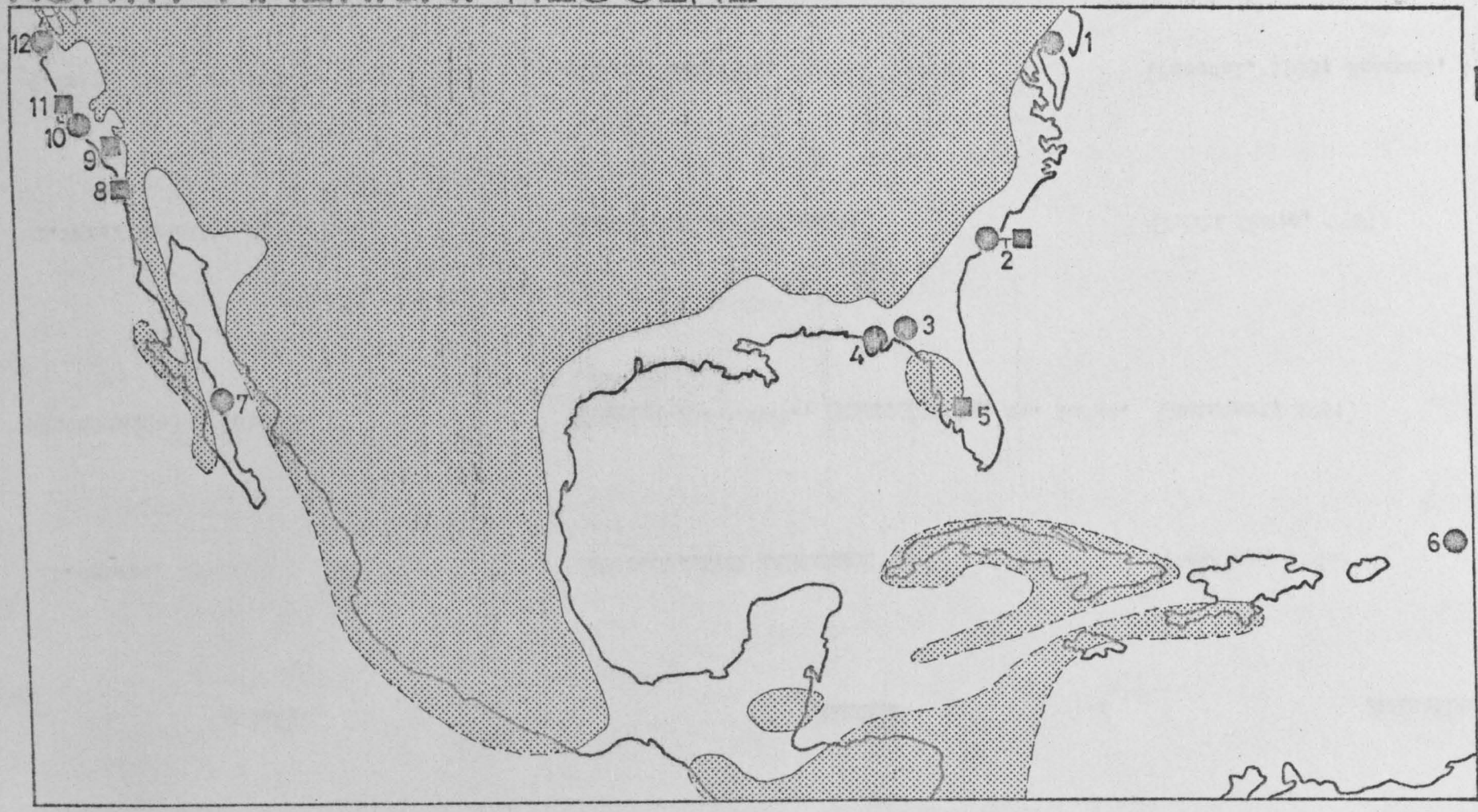
•239•

(adapted from Schuchert, 1955)

KEY TO FIGURE IIIb

Locality	Species	Source(s)
East Coast and Caribbean		
1.Calvert Co., Maryland	*Metaxytherium calvertense*	(Kellogg, 1966)
2.Ashley River, South Carolina	*Metaxytherium manigaulti* (Miocene), *Felsinotherium alleni* (Pliocene)	(Cope, 1883) (Simpson, 1932)
3.White Springs, Florida	*Halitherium* sp. nov.	(R. Reinhart, pers. comm.)
4.Quincy, Florida	*Metaxytherium crataegensis* (see Chap.4)	(Simpson, 1932)
5.Mulberry, Florida	*Felsinotherium floridanum*, *F. ossivallense*	(Hay, 1922; Simpson, 1932)
6.Sombrero Is., Lesser Antilles	sirenian indet.	(Lydekker, 1887)
West Coast		
7.La Purisima, Baja California	*Metaxytherium allisoni*	(Kilmer, 1965)
8.San Diego Co., California	*Hydrodamalis* sp. nov.	(Domning, 1970a)
9.Orange Co., California	*Hydrodamalis* sp. nov.	(Domning, 1970a)
10.Santa Barbara Co., California	*Metaxytherium jordani*	(Kellogg, 1925)
11.San Luis Obispo Co., California	*Hydrodamalis* sp. nov.	(Domning, 1970a)
12.Santa Cruz Co., California	*M. jordani*	(Kellogg, 1925)

FIG. IIIb
NORTH AMERICA: NEOGENE

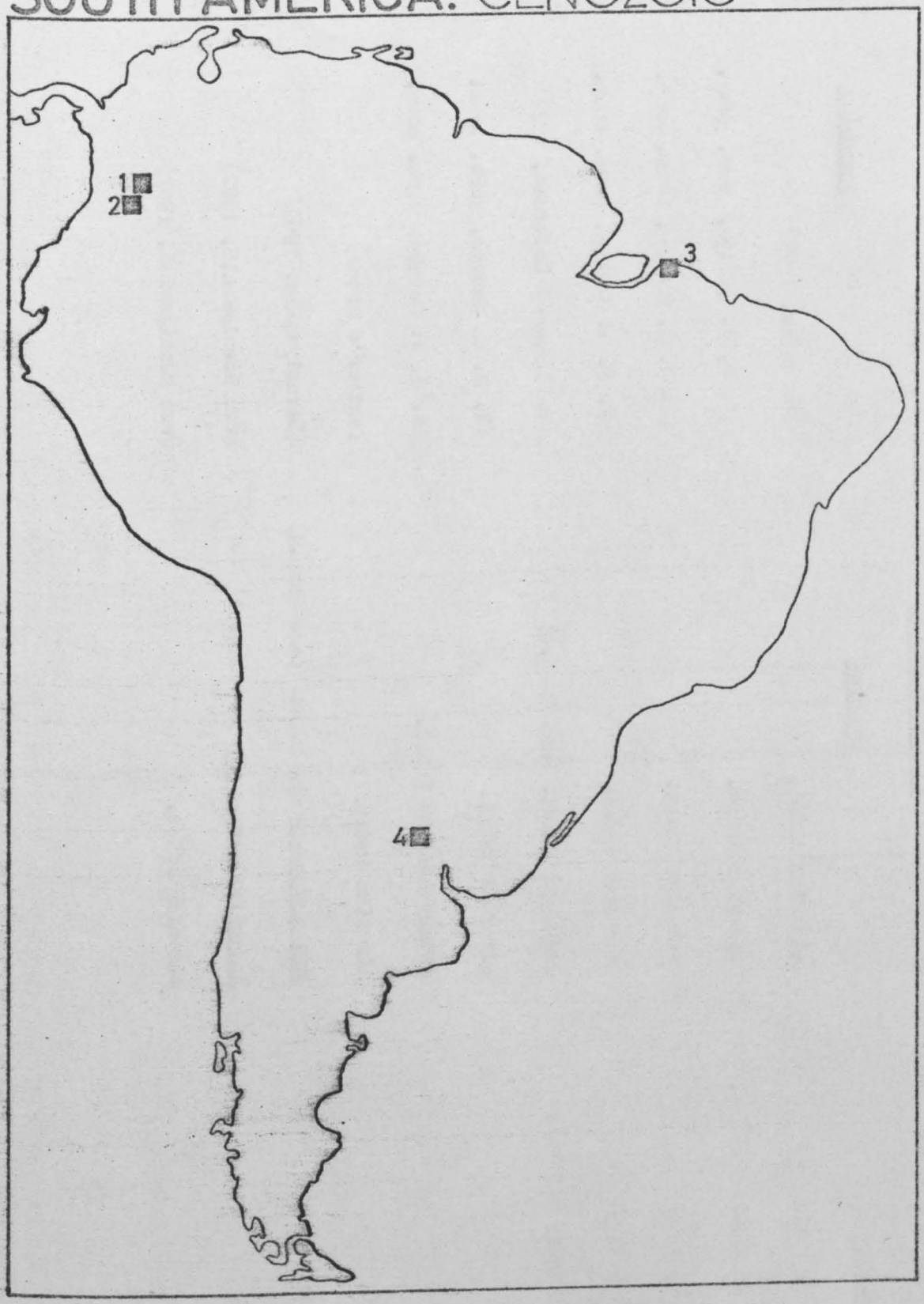


(adapted from Schuchert, 1955)

KEY TO FIGURE IV

Locality	Species	Source(s)
1.Ortega, Colombia	*Metaxytherium ortegense*	(Kellogg, 1966)
2.Villavieja, Colombia	*Ribodon* sp. indet., *Metaxytherium* sp. indet. (see Chap.3)	(Reinhart, 1951)
3.Para, Brasil	*Sirenotherium pirabense*	(Paula Couto, 1967)
4.Entre Rios, Argentina	*Ribodon limbatus*, dugongid indet.	(Pascual, 1953; Pascual, 1966)

FIG.IV
SOUTH AMERICA: CENOZOIC



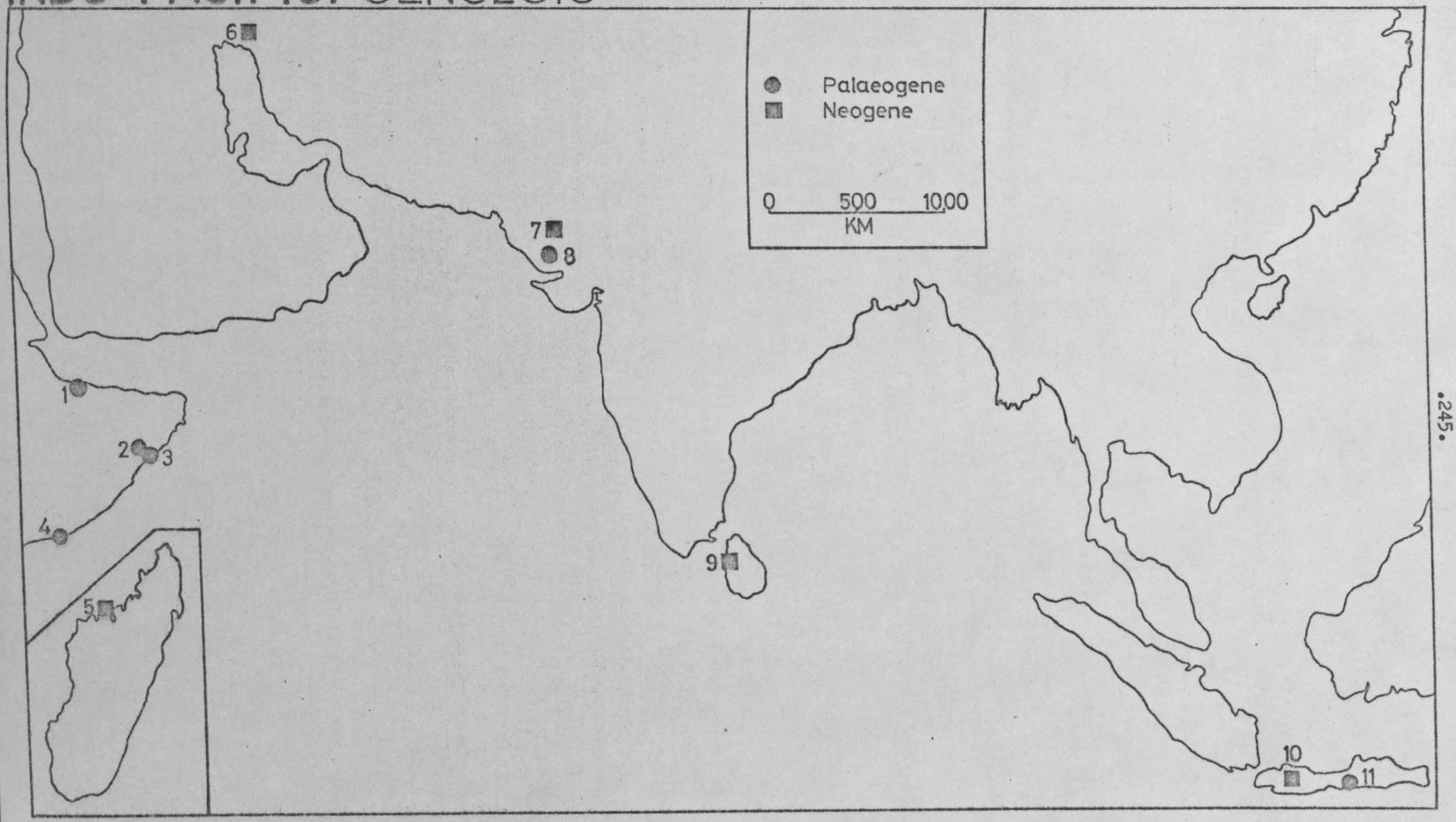
■ Neogene

0 500 1000
KM

KEY TO FIGURE V

Locality	Species	Source(s)
1.Daban, Somali Republic	sirenian indet.	(McFadyen, 1952)
2.Callis, Somali Republic	sirenian indet.	(R. J. G. Savage, pers. comm.)
3.Bedei, Somali Republic	sirenian indet.	(R. J. G. Savage, pers. comm.)
4.Mogedishu, Somali Republic	sirenian indet.	(R. J. G. Savage, pers. comm.)
5.Ile Makamby, Malagasy Republic	dugongid indet. (see Chap.4)	(Collignon & Cottreau, 1927)
6.Agha Jari, Iran	sirenian indet.	(R. J. G. Savage, pers. comm.)
7.Kutch, India	metaxytheriine indet.	(R. J. G. Savage, pers. comm.)
8.Matanomadh, India	sirenian indet.	(author's notes)
9.Dutch Bay, Ceylon	*Metaxytherium* sp. indet. (see Chap.4)	(Deraniyagala, 1969)
10.Njalindung, Java	*Indosiren javanensa* (see Chap.4)	(von Koenigswald, 1952)
11.Manggulan, Java	sirenian indet.	(von Koenigswald, 1952)

FIG.V
INDO-PACIFIC: CENOZOIC



PART TWO

SIRENIAN FEEDING MECHANISMS

INTRODUCTION

The two surviving sirenian genera, Trichechus and Dugong, are very specialized as aquatic herbivores, and represent two lineages that have undoubtedly been separate since at least the Eocene (Simpson, 1932). This divergense has resulted in two different, albeit efficient, methods for dealing with the plants upon which these animals feed. Whereas the dugong feeds principally on submerged vegetation (the so-called "dugong grasses"), it is known that the manatee prefers floating vegetation such as the water hyacinth (Eichhornia crassipes Solms). The numerous osteological differences between Trichechus and Dugong have been tabulated by Simpson (1932), and they are especially prominent in the head region. By far the most important differential features are the deflected rostrum of Dugong, and the presence in that genus of a reduced dentition rather than the increased number of cheek teeth characteristic of Trichechus. In Chapter 4 of Part 1 it was demonstrated that the deflected rostrum of the dugong was most probably developed as a response to the animal's need to procure its particular food; therefore these generic differences of the skull and mandible are intimately connected with the feeding mechanisms of the manatee and dugong.

The availability to me of a preserved dugong head meant that I could investigate the jaw musculature of this genus. Although the unusual structure of the dugong's skull and mandible has been frequently mentioned in the literature, nobody has attempted to relate it to the soft tissues visible on a preserved specimen. The marked downward flexure of the premaxillae and the mandible suggests an unusual method of mastication that must be unique to the Dugongidae amongst the mammals. In order to understand how these remarkable modifications of the skull are integrated with the process of mastication it is necessary to study the internal structure of the buccal cavity and the arrangement of the jaw muscles. Unfortunately, no head of a manatee was available for dissection, but it is possible to trace most of the muscle origin and insertion areas by comparing its skull and mandible with those of the dugong. Since both living genera are believed to have originated from

Eocene (or maybe even pre-Eocene) ancestors, the skull of an Eocene sirenian has been studied to get some idea of the disposition of its jaw musculature. The extrapolation of information from living animals to their extinct relatives is always a very hazardous pursuit, but the Eocene sirenians of the families Protosirenidae and Eotheroididae are sufficiently well known to enable a cautious comparison to be made with the two living genera.

The specimen available to me for dissection, the head of an adult male dugong, was obtained from the Department of Zoology, James Cook University of North Queensland, Townsville, Queensland, Australia, through Drs. G. C. L. and C. K. R. Bertram of Cambridge. This dugong had been collected in September, 1965, near Magnetic Island, Horseshoe Bay, Queensland. The skulls used to map the origin and insertion areas of the different muscles and to measure the lever arms and correction factors were BM(NH) 1946.8.6.4 (an adult female *Dugong dugon*) and BM(NH) 1950.1.23.2 (*Trichechus senegalensis*).

ABBREVIATIONS FOR FIGURES 1 AND 2

CT	cheek tooth
MP	mandibular pad
MPP	main premaxillary pad
P	palate
T	tongue
UJP	upper jaw pad

CHAPTER 1: THE STRUCTURE OF THE BUCCAL CAVITY OF DUGONG

Because the dugong head had been preserved in a drum of salt for more than five years it was very dessicated and had to be immersed in water for two days to aid reconstitution. The head was then put into a preservative fluid made up as follows:

propylene glycol (propane-1, 2-diol)	10.0 parts
formaldehyde (40%)	2.5 parts
tap water	100.0 parts

The jaw muscles had to be dissected before the internal structure of the mouth could be investigated, but this sequence will be reversed in the following account.

The downward deflection of the upper and lower jaws of Dugong produces two distinct surfaces on both the skull and the mandible:

skull
- a) rostral surface (premaxillary pad)
- b) palate

mandible
- c) symphysial surface (mandibular pad)
- d) tongue

a) Rostral surface (Plate 1):

On a prepared skull the ventral surface of the rostrum consists in the main of the premaxillae, but also includes an anterior extension of the maxillae. This rostral surface extends from the distal end of the premaxillae to the posterior border of the incisive foramen, and it is inclined at an angle of 70° to the palate. The surface is transversely concave and forms a trough running from between the incisor tusks onto the palate. In the living animal this depression is filled with tissue so as to form a flat surface - the premaxillary pad.

The premaxillary pad can be divided into two unequal parts that are separated by a transverse V-shaped groove, a small distal component (the "upper jaw pad" of Annandale (1905)) and the main part of the pad. The distal

PLATE 1

Premaxillary pad and palate of *Dugong*

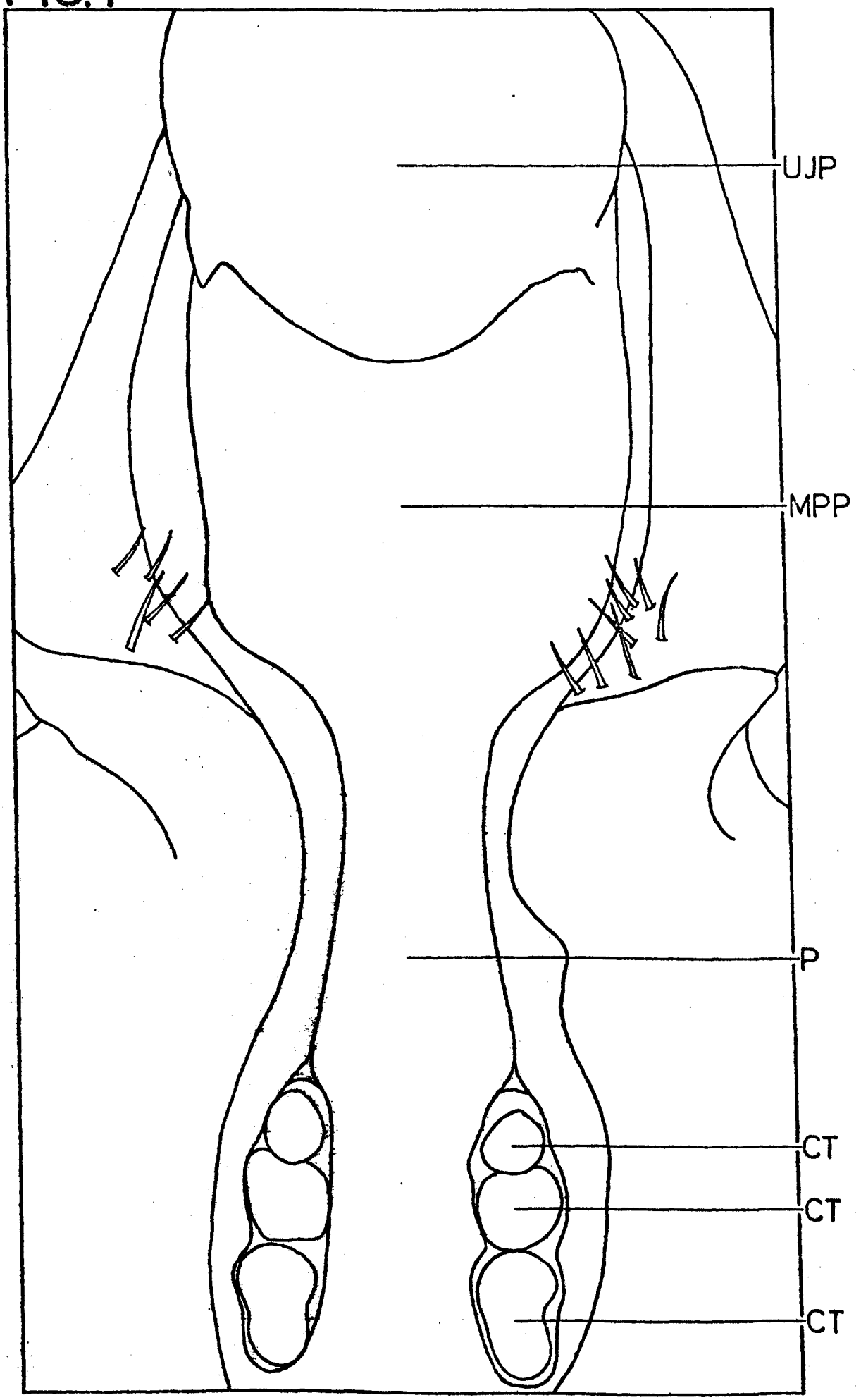
x1.1

FIGURE 1

Drawing of Plate 1

PLATE 1

FIG. 1



component is not supported by the premaxillae and there is therefore a certain degree of flexibility between it and the main part of the pad. The movement of the smaller part is restricted dorsally by the tusks of the male, but it is able to move in towards the buccal cavity. The main part of the premaxillary pad is very solidly backed by the rostral surface of the premaxillae, and it is covered with numerous papillae. These papillae also extend onto the proximal surface of the smaller pad. The spaces between the papillae are densely clothed with short hairs, and the compactness of these two elements gives the premaxillary pad a rasp-like texture.

b) Palate (Plate 1):

The palate extends from the posterior border of the incisive foramen as far as the posterior surface of the last cheek tooth. It is narrower than the rostral surface and its covering tissue is not so firm. Papillae are restricted to the region adjacent to the premaxillary pad, and there are no interstitial hairs. The area between the cheek teeth is ridged, but the pattern of these ridges is faint. The occlusal surfaces of the peg-like cheek teeth are almost level with the palate, and, because they are devoid of enamel, they are very worn.

c) Symphysial surface (Plate 2):

The mandibular symphysis is robust and ventrally deflected, with the two halves of the mandible being firmly fused. The flat symphysial surface makes an angle of 70° with the dorsal margins of the horizontal rami, and in most specimens there is no trace of the incisor-canine dentition on it apart from the partly filled alveoli. The area of the symphysial surface is increased by lateral flanges that are most prominent proximally. The surface is basically oval, but its proximal edge is notched to receive the tip of the tongue and its distal edge is slightly elongated. The pad that covers the symphysial surface is very firm - it will be referred to as the mandibular pad. The surface of the pad bears an arrangement of grooves and ridges that is imposed upon it by the contours of the underlying bone. The

PLATE 2

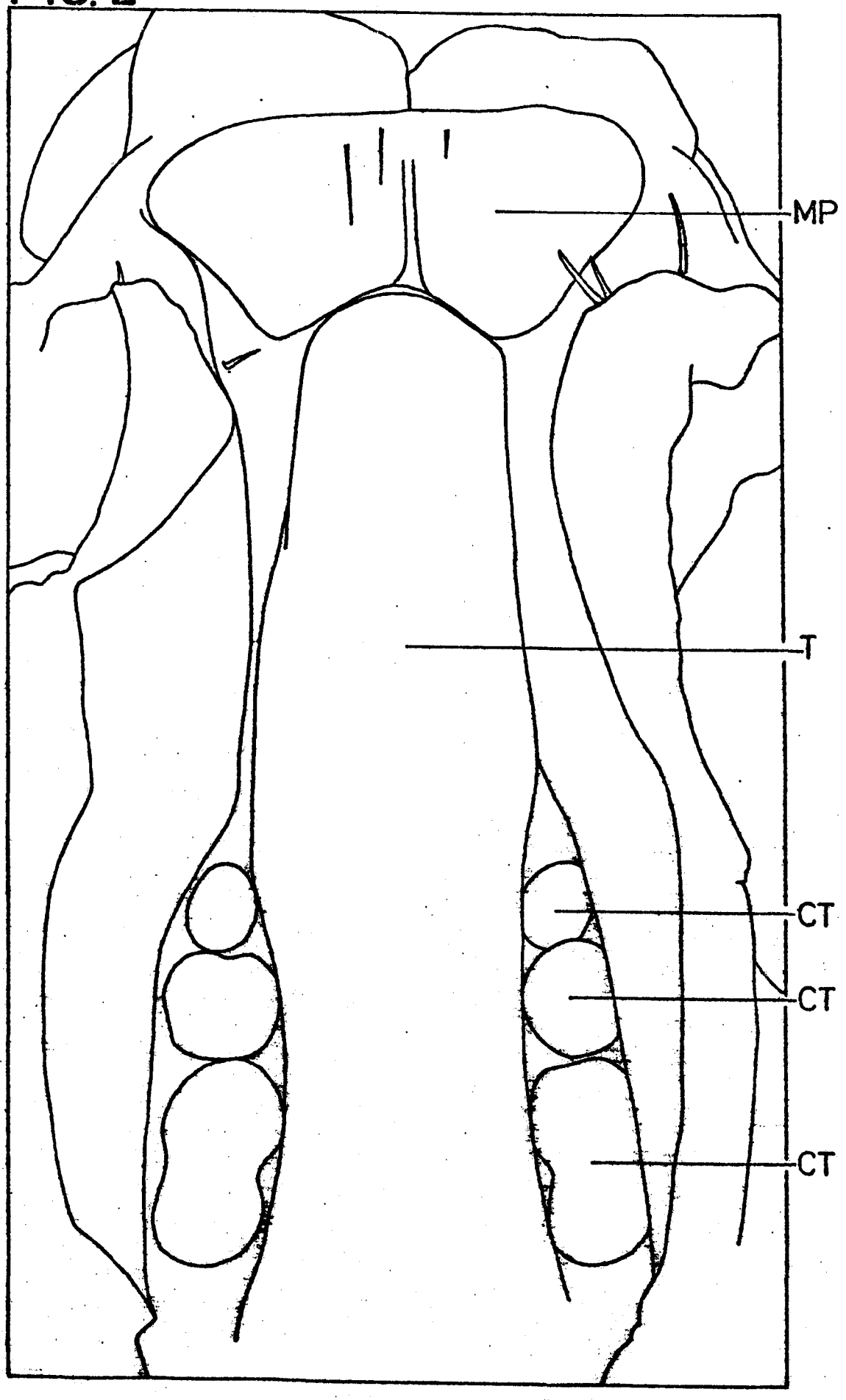
Mandibular pad and tongue of *Dugong*
x1.6

FIGURE 2

Drawing of Plate 2

PLATE 2

FIG. 2



pad is covered with papillae that are much denser than those on the premaxillary pad, and their compactness gives a flatter surface than on the latter.

d) Tongue (Plate 2):

The gap between the horizontal rami is completely filled by the long, slender tongue. The tongue is thick and has a well-developed musculature that reaches to within 13mm of its tip. Because of this rigid anchoring of the tongue in the symphysial region it could not have been protrusible. The surface of the tongue has a velvety texture, and in life it would lie above the level of the occlusal surfaces of the cheek teeth.

Distribution of hair on the face of Dugong

Gohar (1957) found three distinct types of hair on the heads of dugongs from the Red Sea, and he gave a detailed description of each type. The head that I examined showed all three types, each of which was restricted to a specific area:

(a) The largest hairs are very robust structures that are as much as 2mm in diameter. On the upper jaw they are most numerous on the lower part of the facial disc, and they are arranged in alternating rows. On the lower jaw they are limited to the area of the lip that is anterior to the mandibular pad; the size of the hairs decreases proximally and they also appear to alternate from row to row.

(b) Smaller hairs, c.1mm in diameter, are abundant on the internal surface of the cheek between the premaxillary and rostral pads. They are directed anteriorly and are much denser than the larger hairs.

(c) Relatively normal-sized hairs, c.0.3mm in diameter, are very sparsely distributed over the head, but they are most numerous on the chin. This is the type of hair that is also found on the body and limbs.

The hairs of groups (a) and (b) can satisfactorily be termed vibrissae because of their size and position on the face. The vibrissae of Trichechus

have been shown to be typical sinus hairs, i.e. tactile hairs (Woodard, 1969); it is therefore reasonable to assume that the vibrissae of Dugong also serve some tactile sensory function.

CHAPTER 2: THE JAW MUSCULATURE OF DUGONG AND OTHER SIRENIANS

Before being put into the drum of salt, the dugong head had been prepared so that the salt could penetrate the flesh. This had entailed separating most of the skin from the head and making incisions in the muscles, damaging the latter in the process. The left side of the head was used for the dissection of the jaw muscles because it had suffered the least damage during the preparation.

The dissection was hindered at first by a thick layer of decomposed blubber that covered the muscles, but most of this fatty layer was removed by using a commercial detergent to emulsify it.

Musculus (M.) masseter (Figures 4A and 4B):

Dugong

The masseter is exposed upon removal of the M. zygomaticus. Its two divisions, the pars superficialis and the pars profunda, have separate origins on the zygomatic arch, but their fibres merge ventrally and they have a common insertion on the mandible. The origin of the superficial masseter extends for the whole length of the ventral surface of the jugal component of the zygomatic arch. The area of attachment is narrow for most of its extent, but it widens anteriorly where the surface of the bone is more rugose. This external division of the masseter is short and thick, and it exists as a distinct muscle block for only about two-thirds of the distance down the ascending ramus until it merges with the underlying deep masseter. The superficial masseter covers the deep masseter for most of its spread except for a small area adjacent to the neck of the mandibular condyle.

The deep masseter originates on the ventral surface of the jugal, but medial to the origin of the superficial masseter. Unlike the latter it has a very short attachment area that only occupies the anterior half of the jugal. This area is wider than that of the superficial masseter, although

posteriorly it is situated on the medial surface of the bone rather than the ventral surface. Therefore the effective origin of both divisions of the masseter is restricted to the thickened part of the jugal beneath the orbit. The deep masseter fans out from its origin until it covers the entire posterior part of the mandible. Both divisions have their insertions on a broad area enclosed ventrally by the angular process of the mandible. The mandibular angle bears prominent muscle scars that would assist in firmly attaching the masseter.

The pars superficialis and pars profunda have the same weights, the shortness of the former being compensated for by its thickness.

Trichechus

The area of attachment of the masseter to the jugal in this genus is not expanded anteriorly as it is in Dugong. The orbit is situated more anteriorly than in Dugong, and the origin of the masseter is located behind the orbit rather than directly beneath it. The masseter has an insertion on the mandible that is similar in shape to that of Dugong, although it is smaller in area.

Eocene sirenians

The zygomatic arches of Eotheroides, Protosiren, and Libysiren are very robust and are intermediate in shape between those of Dugong and Trichechus. The attachment area of the masseter to the jugal is narrow and is situated behind the orbit. The area of insertion onto the mandible is enlarged because there is a posterior extension to the vertical ramus of the mandible that is limited dorsally by a projection at the level of the alveolar margin. This projection has been retained, in a rudimentary fashion, by the two living genera, although it has almost vanished in Dugong.

M. temporalis (Figures 4A-C):

Dugong

The temporal muscle is smaller than either of the divisions of the

masseter. Its origin is on both the parietal and the squamosal, the area of attachment being the lateral surface of the parietal and the dorsal surface of the lateral wing of the squamosal. The muscle inserts onto both sides of the coronoid process of the mandible, with the most extensive attachment being on the lateral side.

Trichechus

The temporal crests are most prominent on the frontals, and overall they are closer together than in Dugong. The zygomatic process of the squamosal is more massive than in Dugong, and may therefore have had a closer relationship with the temporal muscle. The coronoid process of this genus is very different from that of Dugong - in the latter genus each process is almost vertical, tapered distally, and its highest point lies above the level of the mandibular condyle; whereas in Trichechus the process is directed anterodorsally, not tapered distally, and its highest point lies below the condyle. The lateral and medial insertion areas on the coronoid process are smooth in the specimen of Dugong examined, but in the specimen of Trichechus they are ridged to provide a more intimate union between the bone and muscle.

Eocene sirenians

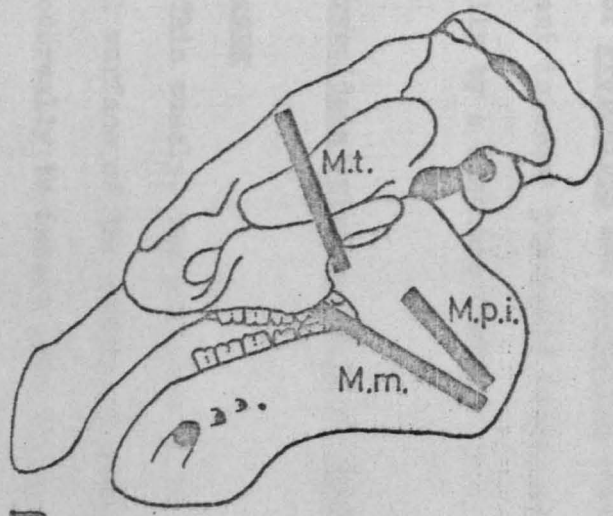
The slight temporal crests of Eotheroides and Protosiren give the braincase an angular aspect (cf. Dugong), but the braincase of Libysiren does not bear crests and is rounded transversely. The coronoid processes of Eotheroides, and apparently those of protosirenids also, are very similar to those of Dugong. The temporal muscles must therefore have closely resembled those of Dugong.

M. pterygoideus internus (Figures 4D-E):

Dugong

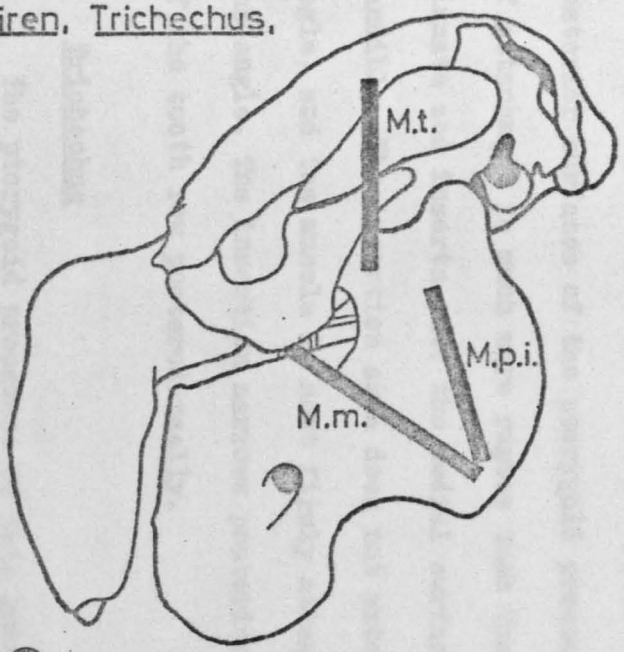
Both pterygoid muscles originate on the well-developed pterygoid process. This process is divided into two distinct parts by a broad

FIG. 3 Orientation of main jaw-closing muscles of Protosiren, Trichechus, and Dugong (solid lines indicate muscle lengths)

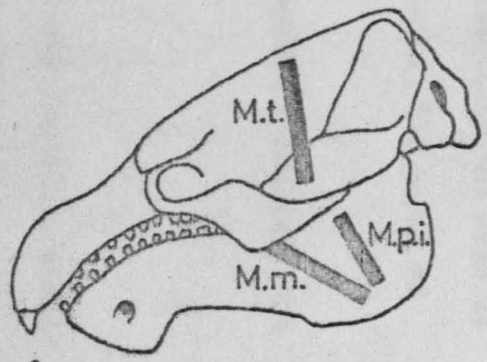


B. Trichechus

all x1/4



C. Dugong



A. Protosiren

posterior groove, and the pterygoid muscles are attached to the more lateral part.

The origin of the internal pterygoid muscle is on the ventral and posterior surfaces of the pterygoid process's lateral division, and the area of attachment is much more rugose than the surrounding bone. The muscle is pinnate and inserts onto the medial surface of the vertical ramus of the mandible. The insertion area does not extend anterior to the mandibular angle, and the muscle is most firmly attached in a small concavity behind the angle. The insertion narrows posteriorly and almost reaches the level of the tooth row posterodorsally.

Trichechus

The pterygoid processes of this genus are fundamentally the same as those of Dugong in shape, and, as far as can be estimated, the areas of origin of the pterygoid muscles are similar also.

The insertion area of the internal pterygoid muscle is smaller, but more precisely delineated, than in Dugong.

Eocene sirenians

The pterygoid processes of Eotheroides are thin and lamellar, unlike those of Protosiren and Libysiren which are stout. However, both groups have prominent internal pterygoid fossae on the mandible that are bordered ventrally by a distinct shelf.

M. pterygoideus externus (Figures 4D-E):

Dugong

This muscle, the smallest to be considered, originates from the lateral surface of the pterygoid process's lateral division. It passes posterodorsally to insert onto the medial surface of the neck of the mandibular condyle. The area of insertion is smaller than the area of origin, and, because of the positioning of these two areas, the external pterygoid muscle is almost horizontal.

Trichechus

The origin and insertion areas of this muscle cannot be accurately traced on the skull and mandible of Trichechus, but it is assumed that the muscle was not drastically different from that of Dugong.

Eocene sirenians

As for Trichechus.

M. digastricus (Figures 4A-D):

Dugong

In most mammals the digastric muscle consists of two muscular "bellies" separated by a dividing tendon - the anterior "belly" being innervated by the fifth nerve, whilst the posterior "belly" is innervated by the seventh. In the living sirenians and some other mammals (e.g. marsupials, carnivores, bats etc.) this muscle is classed as a M. digastricus spurius, in which the two "bellies" form a single muscle mass divided by a tendinous intersection (Grassé, 1968). In mammals with a M. digastricus spurius the muscle is attached to the mandible by the equivalent of the original anterior "belly".

The digastric muscle of Dugong originates as a thick tendon on the ventral surface of each paroccipital process. The tendon is c.25mm in length, and it gives rise to a very fleshy pinnate muscle. The small area of insertion on the mandible is in the region of the mandibular angle, but anterior to the insertion of the internal pterygoid muscle. An attachment also occurs along the posteroventral edge of the mandible. For most of its extent the fleshy portion of the digastric overlies the internal pterygoid.

Trichechus

In this genus the paroccipital processes are smaller and farther apart than in Dugong, and the origin of the muscle is on the ventrolateral surface of each process. The insertion cannot be traced with any degree of certainty on the bone of the mandible.

FIGURE 4

JAW MUSCULATURE OF DUGONG

A. Lateral view of skull and mandible showing superficial dissection

B. The same, with M. masseter pars superficialis removed

C. The same, with the entire M. masseter removed

D. Sagittal section of skull and mandible showing superficial dissection

E. The same, with M. digastricus removed

5cm

FIG. 4

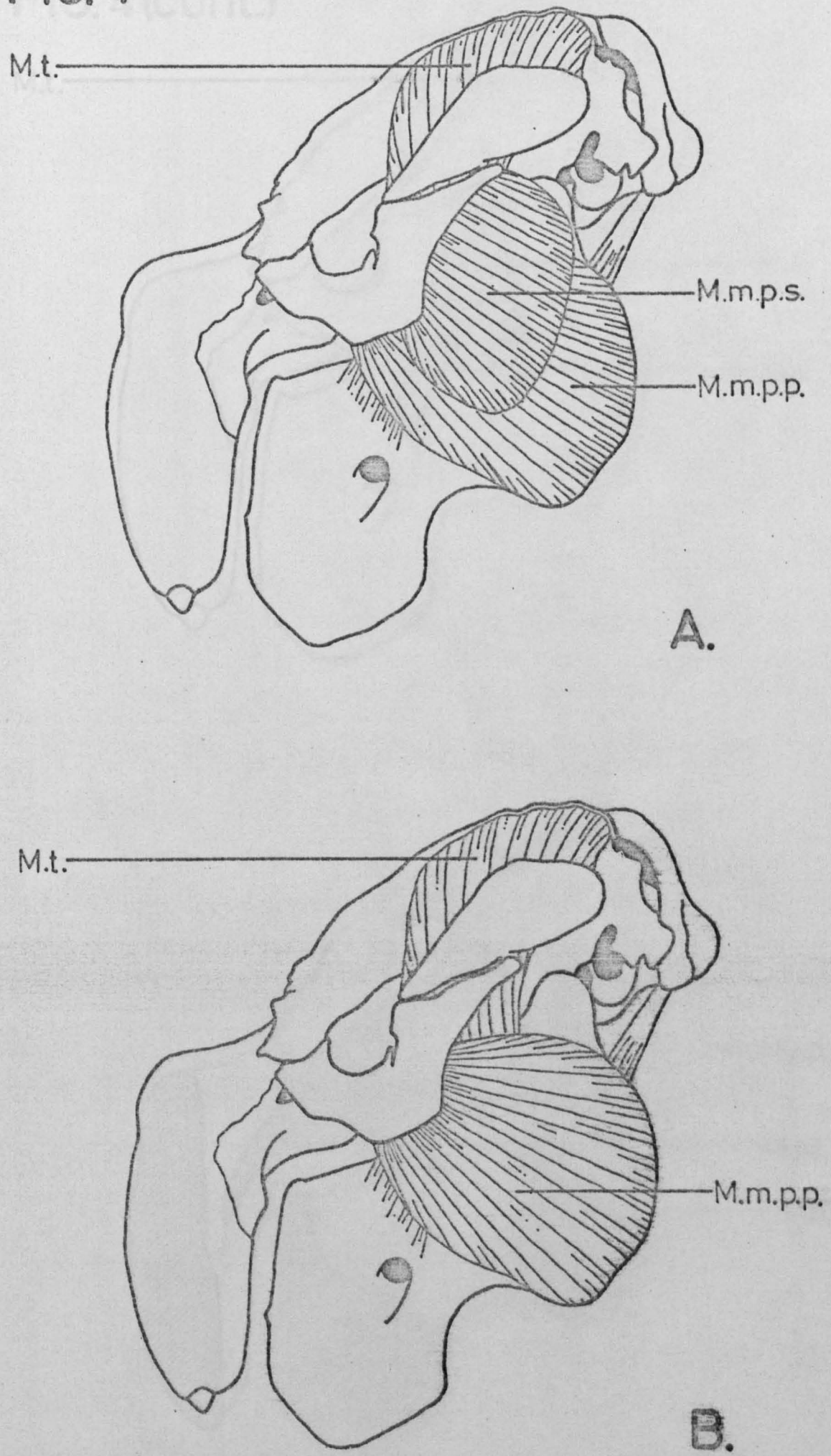
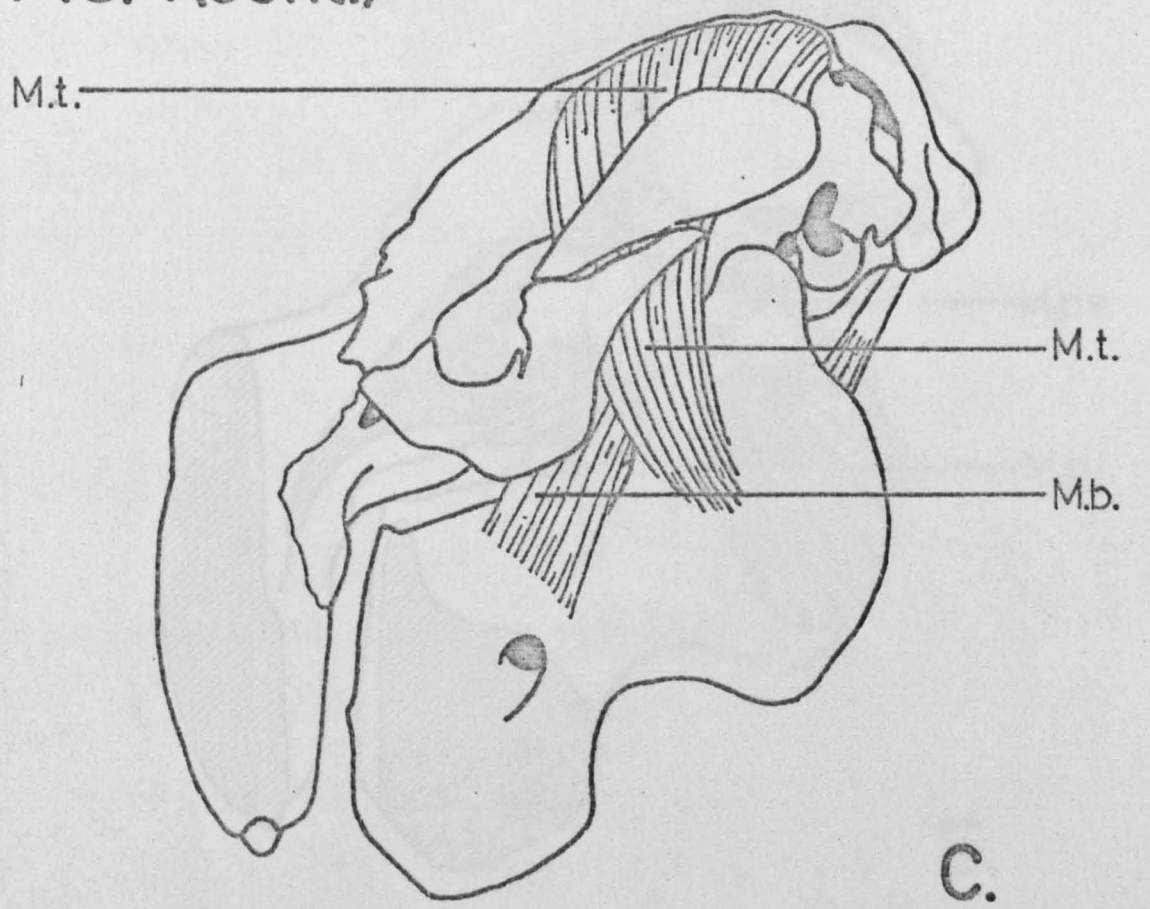


FIG. 4 (cont.)



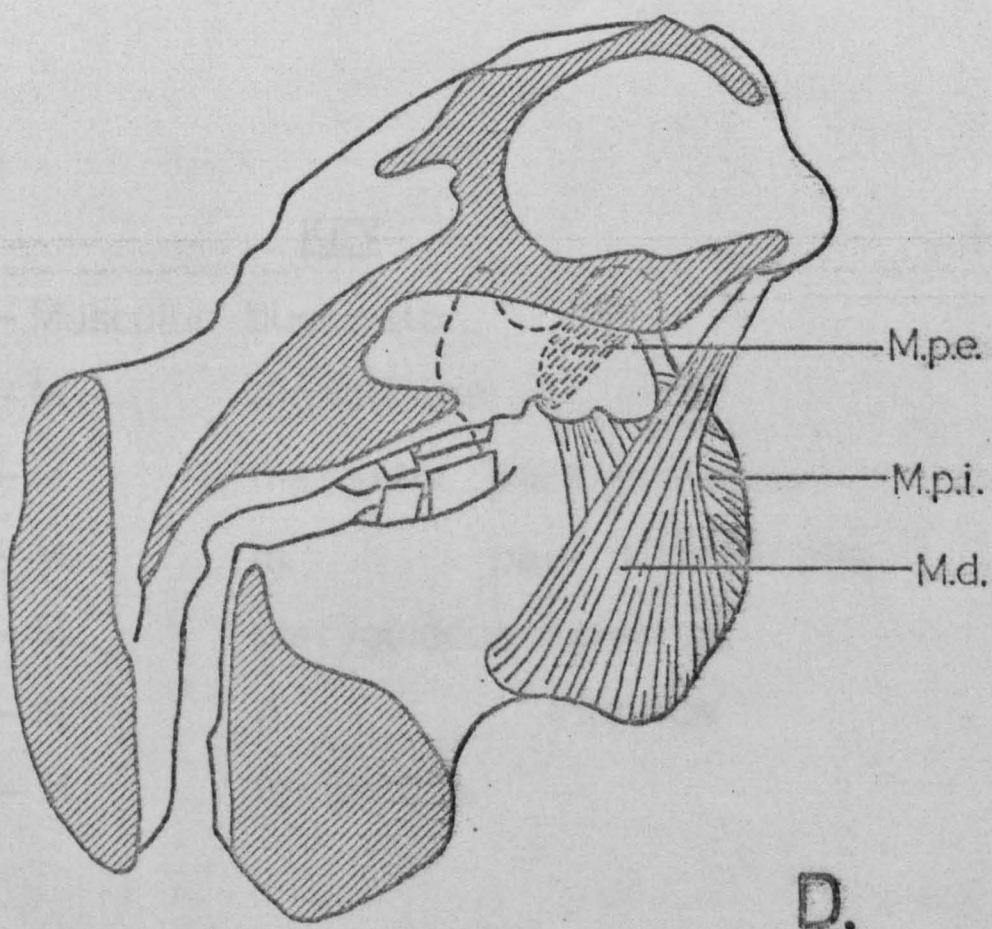
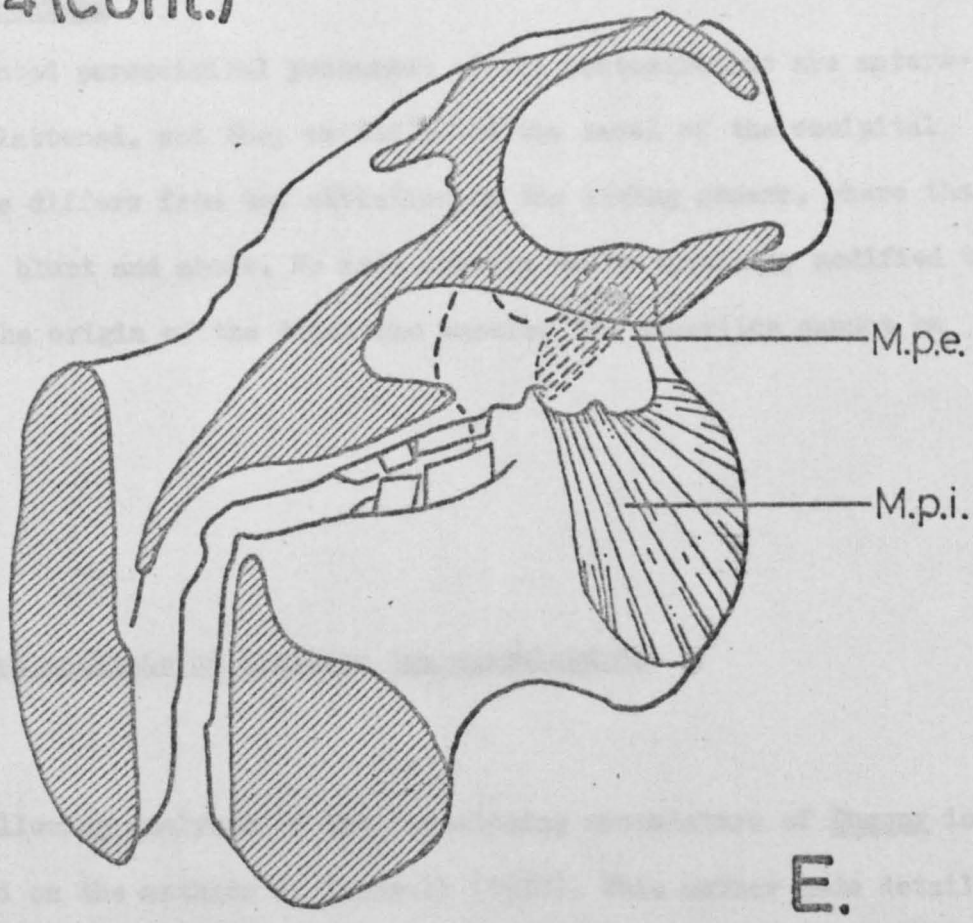


FIG. 4 (cont.)



KEY

M.b.	— Musculus	buccinator
M.d.	— M.	digastricus
M.m.p.p.	— M.	masseter pars profunda
M.m.p.s.	— M.	m. pars superficialis
M.p.e.	— M.	pterygoideus externus
M.p.i.	— M.	p. internus
M.t.	— M.	temporalis

Eocene sirenians

The pointed paroccipital processes of the protosirenids are antero-posteriorly flattened, and they extend below the level of the occipital condyles. This differs from the situation in the living genera, where these processes are blunt and short. No area appears to be specially modified to function as the origin of the digastric muscle. The insertion cannot be traced.

The functional analysis of sirenian jaw musculatures

Dugong

The following analysis of the jaw-closing musculature of Dugong is largely based on the methods of Turnbull (1970). This author made detailed dissections of the jaw musculature of nine representative mammalian genera and used his observations and measurements to construct a simple power formula. This formula makes use of muscle mass (weight or volume), muscle position and cross-sectional thickness, leverages, and direction of muscle pull. Taking all of these factors into consideration, the useful power (E) of the jaw-closing mechanics for each muscle can be expressed thus (Turnbull, 1970, p. 282):

$$E = M \times F_L \times F_X \times r$$

M = mass (weight or volume) of muscle group expressed as % of total jaw-closing musculature

F_L, F_X = correction factors (sine functions of the angles that the muscle axis makes with the longitudinal and transverse planes of the skull respectively)

r = ratio of the mechanical advantage of the effort lever arm in relation to the resistance lever arm

The power thus calculated can be represented diagrammatically on drawings of the skull and mandible, together with the muscle attachment areas, lever arms, and resultants at the condyle (see Figure 5).

Turnbull noted that, when comparing the measured muscle mass with the

TABLE 1

i) Weights and percentages of masticatory muscles

	Weight (in gms)	%	% (without digastric)
M.m.	266.2	53.4	60.0
M.t.	96.4	19.4	22.0
M.p.e.	18.1	3.6	4.1
M.p.i.	60.5	12.2	13.9
M.d.	56.7	11.4	—
TOTALS	497.9	100.0	100.0

ii) Useful Power of masticatory muscles

	At cheek teeth	At jaw pads
E_m	60.0	34.0
E_t	6.0	3.4
E_{pe}	0.1	0.1
E_{pi}	2.7	1.5
TOTALS	68.8	39.0

iii) Comparison of Measured Muscle Mass with Calculated Useful Power Values (%)

	Muscle Mass (%)	Useful Power (%)	Change in (% points)	Prop. Change (%)
M.m.	60.0	87.1	+27.1	45% gain
M.t.	22.0	8.7	-13.3	60% loss
M.p.	18.0	4.2	-13.8	77% loss
TOTALS	100.0	100.0	00.0	

calculated useful power values, care must be taken when interpreting the magnitude of the proportionate change. After looking at the results obtained from a large selection of mammals he concluded that only proportionate changes over 20% have any functional significance. Referring to Table 1(iii) it can be seen that in Dugong the masseter, temporal, and pterygoid muscles all have significant proportionate changes (in this table the two pterygoid muscles have been incorporated into one group because it makes it easier to compare the results with those of Turnbull (ibid., tables B-E); when the two muscles are considered separately the M. pterygoideus externus has a 95% loss in the fourth column and the M. pterygoideus internus has a 71% loss).

The efficiency of the masseter muscle can be attributed in the main to the length of its effort lever arm and to the fact that both correction factors are close to 1.0. The dominance that this muscle exhibits over the others in the weight table is enhanced even further when the useful power is considered (see Table 1(iii)). The masseter is without doubt the most important jaw-closing muscle of Dugong, producing nearly four times the useful power at the jaw pads than do the combined efforts of the temporal and pterygoid muscles at the cheek teeth.

The temporal muscle is inefficient because of its relatively short effort lever arm, and because the angles that it makes with the effort lever arm are in the region of 45°. The high proportionate change for the temporal muscle of Dugong is only exceeded in magnitude by that of Equus (70%) out of the very many examples given by Turnbull (ibid., table D).

The pterygoid musculature is even more inefficient than the temporal. The internal pterygoid muscle is very inefficient because its line of action is almost coincident with its effort lever arm. The insignificance of the external pterygoid muscle is due to its extremely short effort lever arm and to the fact that this muscle is almost perpendicular to the medial surface of the neck of the mandibular condyle. The aberrant hyaenid Proteles has a proportionate loss in efficiency of 84% for the pterygoid musculature (Turnbull, ibid., table D). The difference between the proportionate change

values when the pterygoid muscles are considered separately and when they are considered together illustrates the care that must be taken when analyzing jaw musculatures.

Trichechus

When the difference in size is considered it is apparent that the arrangement of the jaw muscles in relation to the skull and mandible is based on the same pattern in both Dugong and Trichechus. However, a distinction of functional importance is present in the disposition of the temporal muscles. The anterodorsal inclination of the coronoid process in Trichechus causes an anterior movement of the insertion of the temporal muscle, and therefore an elongation of the effort lever arm. This increase in the muscle's efficiency is also indicated by the additional development of its origin and insertion areas. Although the masseter muscle does not appear to have suffered reduction, it is evident that it and the temporal muscle are not so unequal in terms of efficiency as they are in Dugong.

The other jaw-closing muscles of Trichechus must be very similar to those of Dugong, although they would all be shorter.

Eocene sirenians

The nonexistence of complete, undistorted, associated skulls and mandibles of the Eocene sirenians makes accurate analyses impossible, but a brief review can be attempted.

The masseter muscle must have been prominent in all of the Eocene genera because its origin and insertion areas are always large. In fact the insertion area was relatively larger in these sirenians than it is in the extant genera.

Because of the similarities between the origin and insertion areas of temporal muscles of the Eocene sirenians and Dugong it is not unreasonable to conclude that the muscles were also similar in gross morphology and function.

The internal pterygoid muscle may have been more important functionally in the Eocene forms because of its prominent insertion area on the

FIGURE 5

ANALYSES OF JAW MECHANICS OF DUGONG

A'. Analysis for M. masseter at cheek teeth
A". Analysis for M. masseter at jaw pads

B'. Analysis for M. temporalis at cheek teeth
B". Analysis for M. temporalis at jaw pads
(insets: reactions at jaw joint x10)

C'. Analysis for M. pterygoideus at cheek teeth
C". Analysis for M. pterygoideus at jaw pads
(insets: reactions at jaw joint x20)

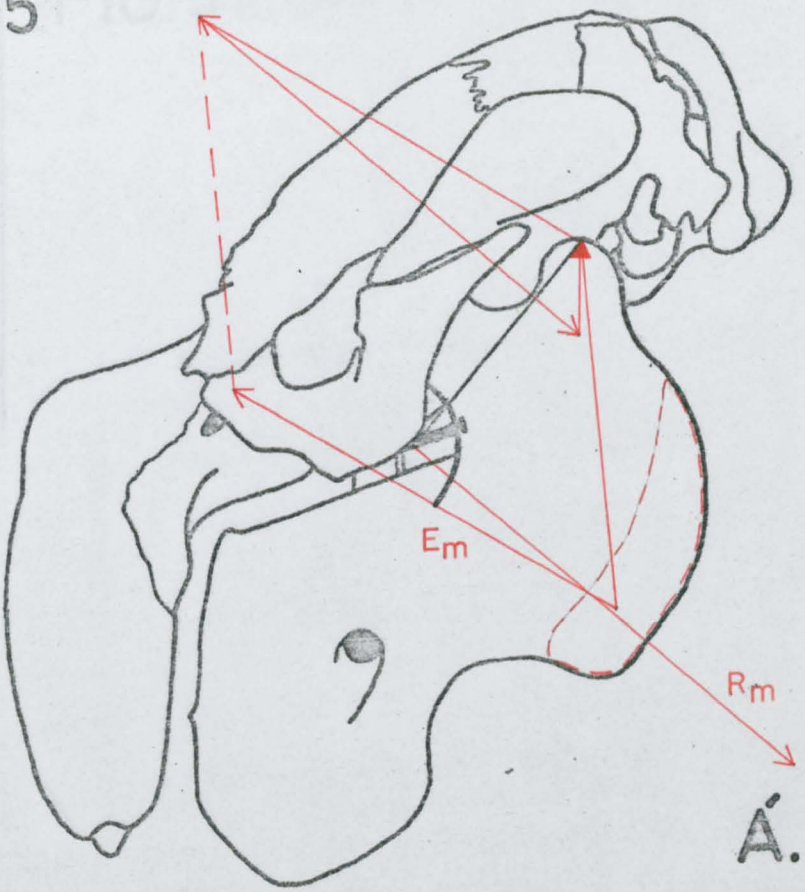
5cm

Abbreviations

E proportioned effort vector

R proportioned resistance vector

FIG. 5



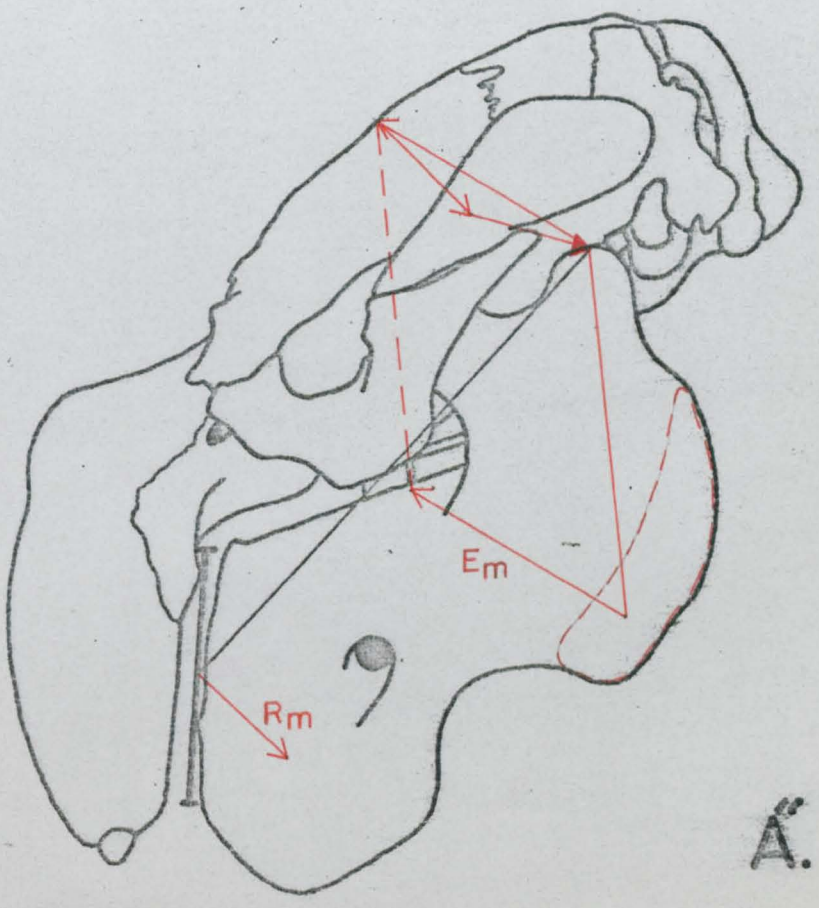
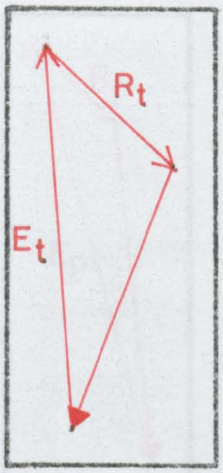
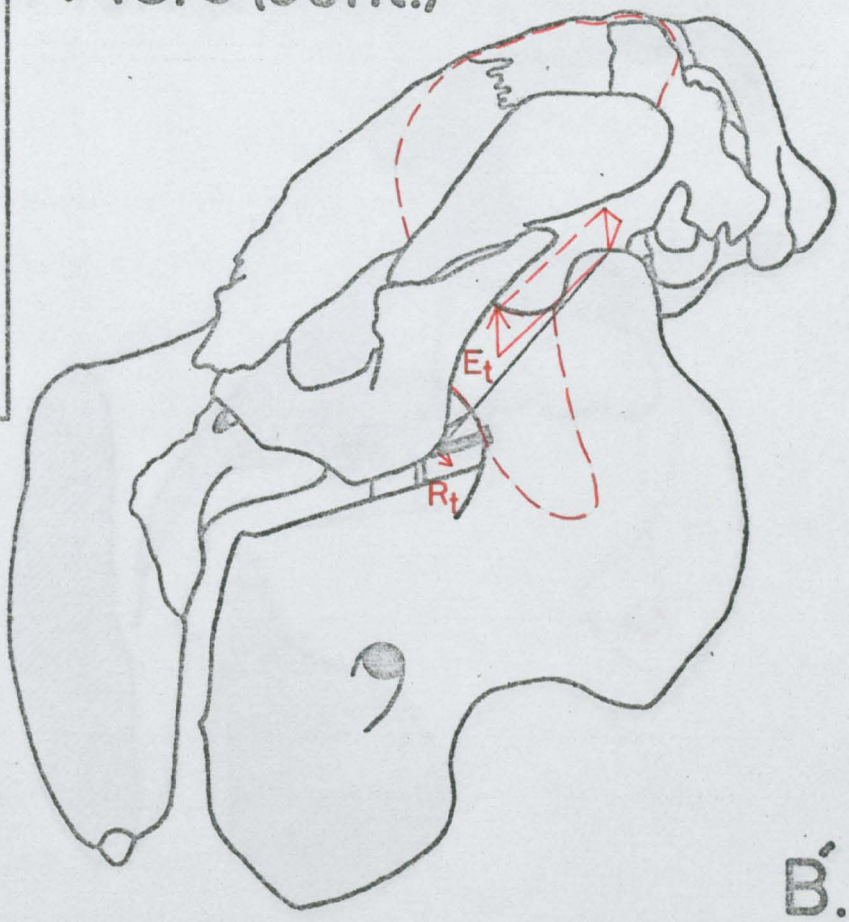
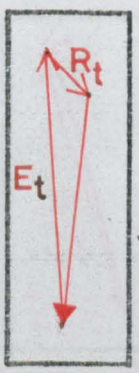


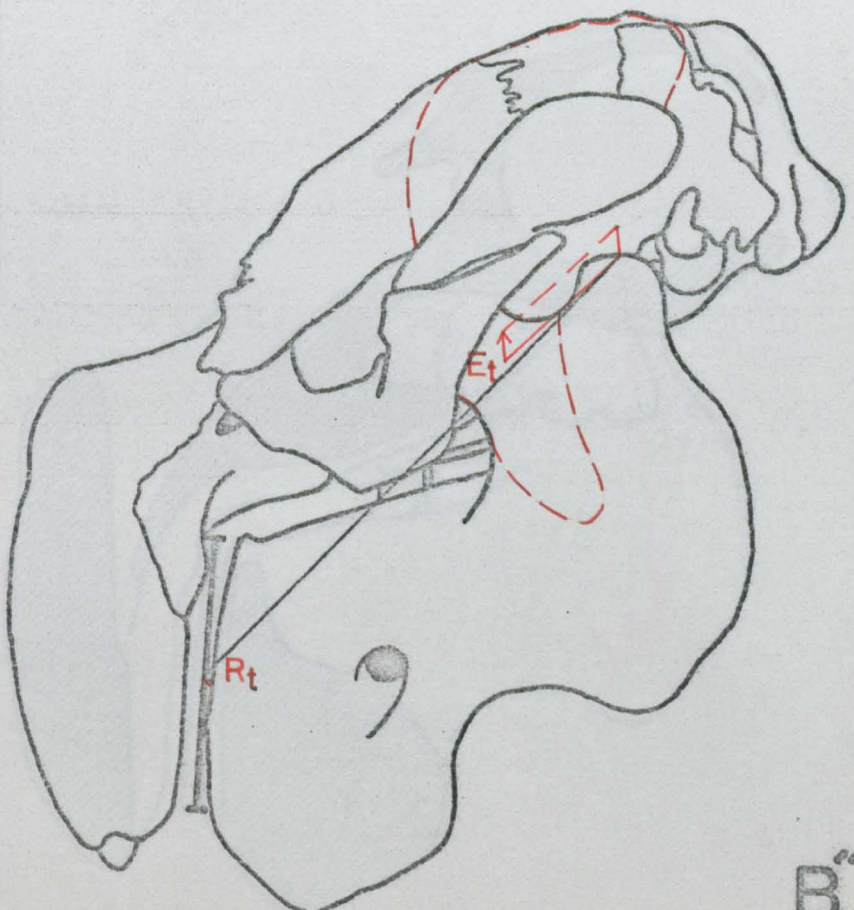
FIG. 5 (cont.)





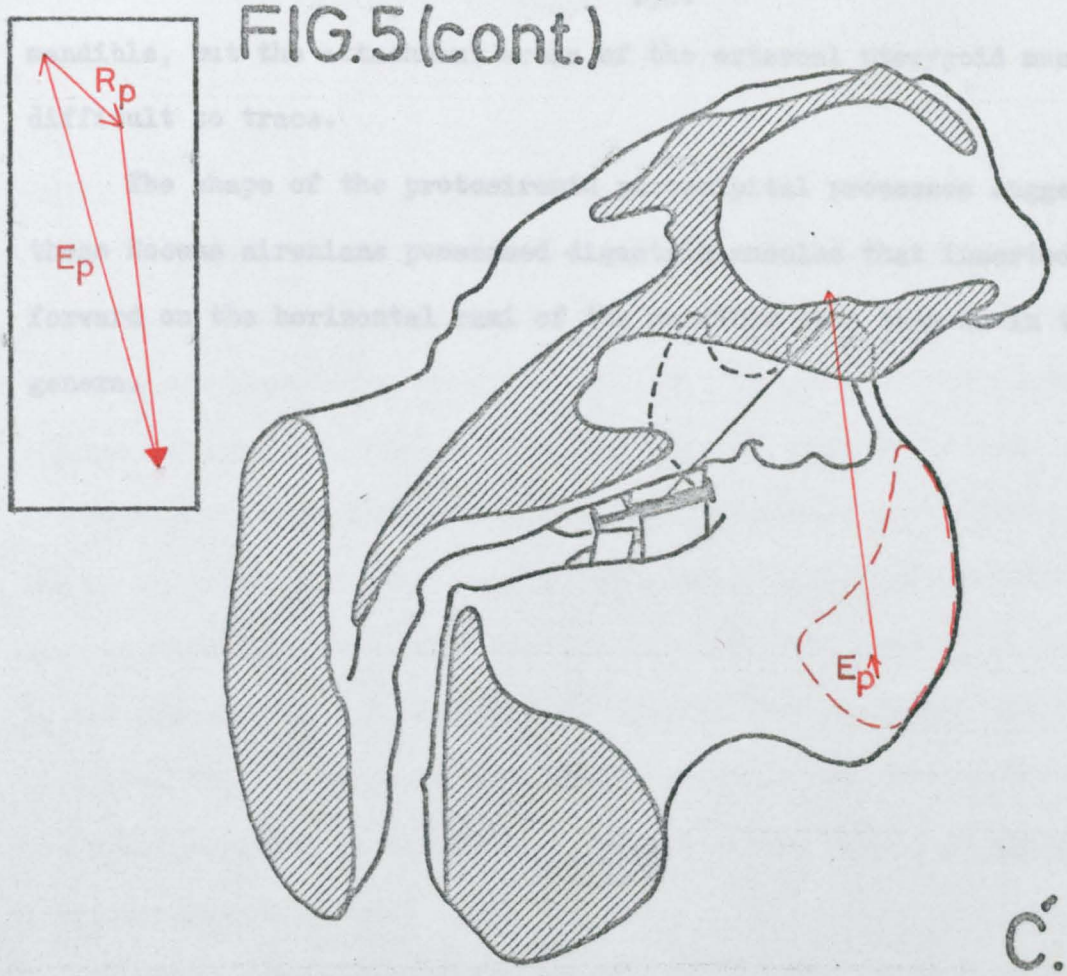
B'.

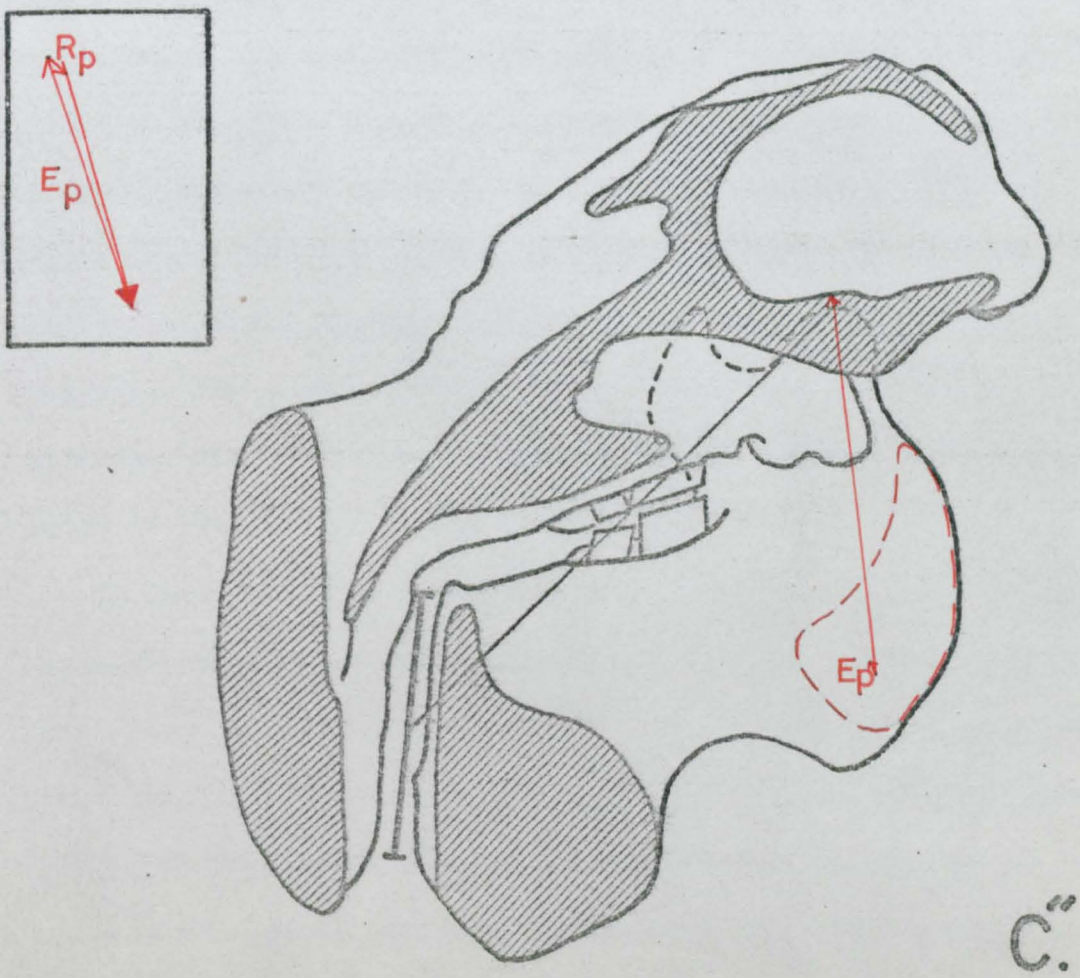




B''.

FIG. 5 (cont.)





mandible, but the attachment areas of the external pterygoid muscle are difficult to trace.

The shape of the protosirenid paroccipital processes suggests that these Eocene sirenians possessed digastric muscles that inserted farther forward on the horizontal rami of the mandible than they do in the living genera.

CHAPTER 3: CONCLUSIONS

Dugong

The analysis in Chapter 2 shows that the masseter muscle is the major jaw-closing muscle of Dugong. A powerful jaw-closing musculature is needed to raise the remarkably heavy mandible as well as to produce a forceful closure of the jaws. The mandible of Dugong is especially massive at the symphysis, the region farthest from the articulation, and this minimizes the need for an efficient jaw-opening musculature - the mandible would be lowered when the jaw-closing muscles relaxed. This suggestion is supported by the presence of a M. digastricus spurius that is weakly attached to the mandible. The insertion of the digastric muscle has moved posteriorly from its usual position at the front of the mandible, and in Dugong it is now inefficiently disposed.

Evidence suggests that the closure of the jaws is by a simple hinge movement, without appreciable fore-and-aft or side-to-side components. Once the jaws are shut there can be little lateral movement between them because the premaxillary and mandibular pads are flush with each other. Their flat surfaces come into contact and prevent any sideways motion; a little lateral movement can occur, however, when the jaws are opened slightly. The cheek teeth do not show any orientated striations that could be attributed to lateral movement because of the absence of enamel on their occlusal surfaces. The glenoid facet is wide and narrow, but bears a cup-shaped articular disc that fits comfortably around the mandibular condyle and thus helps to restrict lateral movement.

If the movement of the mandible is to be restricted to one plane it is necessary to stabilise the lower jaw so that the masticatory pads can always meet squarely. This stabilisation can be achieved by using the temporal, pterygoid, and digastric muscles - all of which are inefficient as jaw-closing or jaw-opening muscles. The contraction of any, or all, of these paired muscles would position the mandible with great precision in relation

to the skull. The temporal and external pterygoid muscles position the coronoid process and condyle respectively, and the internal pterygoid and digastric muscles do the same for the mandibular angle. When the mandible is correctly aligned with the skull, the masseter muscles can be used to close the jaws.

The force exerted on the premaxillary pad by the mandibular pad may be partly absorbed by a kinetic connection that exists between the premaxillae and the rest of the skull. Although most of the cranial sutures of the adult dugong are either fused or firmly interdigitated (Freund, 1908), it is noticeable that the sutures between the premaxillae and surrounding bones (maxillae, jugals, and frontals) are open. Thus the rostrum is not rigidly fixed, but can yield when forces are applied to it in an upwards direction.

The way in which the two masticatory pads are used can only be conjectured at for the present, and studies need to be carried out on living animals. The food plants are probably pushed into the mouth by the flexible tip of the premaxillary pad, and then crushed between the latter and the mandibular pad. The rough, papillated surface of the premaxillary pad and the ridges on the mandibular pad would break up the plant material, making it easier to digest. The tongue, in conjunction with the palate, would then be able to shape the crushed vegetation into boluses that could be easily swallowed. The cheek teeth appear to play no part in the process of mastication because they are without enamel (except when erupting), and therefore have soft occlusal surfaces.

Turnbull (1970) used a jaw-apparatus classification that included five major groups - General Group; Specialised Group I, "carnivore-shear" type; Specialised Group II, "ungulate-grinding" type; Specialised Group III, "rodent-gnawing" type; and Miscellaneous Group. The apparatus of Dugong cannot be placed satisfactorily in any of the first four groups, although there are certain similarities between it and the apparatus of Specialised Group III (e.g. Orycteropus, Cavia). The Miscellaneous Group contains three

ill-defined categories (only two of which may be required when more comparative work has been done), the third of which contains dentally degenerate forms that have developed aberrant masticatory specializations. The unique dentition of the dugong and the singular structure of its masticatory apparatus warrants it being placed in this category.

Trichechus

The differences between the jaw musculatures of Trichechus and Dugong can be related to the different feeding habits of the two genera. The dentition of the adult dugong is reduced to two peg-like teeth on each side, but in the manatee the teeth are bilophodont and supernumerary, erupting in a continuous series throughout the animal's life. Whereas the teeth of the dugong seem to be virtually functionless, those of the manatee are closely connected with mastication. The latter animal does not possess the large premaxillary and mandibular pads that characterize the former, but it does have much smaller pads in these regions.

When the teeth of Trichechus erupt, each one bears two transverse lophs that are gradually worn flat as the tooth moves forwards along the mandible. In well-used (i.e. the most anterior) teeth it is noticeable that the lingual side of the worn occlusal surface is higher than the labial side in the lower jaw, and vice versa in the upper jaw. This is similar to the wear described for the teeth of Dendrohyrax (Maynard Smith & Savage, 1959, fig. 4c). In Trichechus, as in Dendrohyrax, the lower dental arcade is narrower than the upper; therefore the cheek teeth are in occlusion on one side only during mastication. The masticatory stroke is probably similar in the two genera, i.e. more nearly vertical than lateral, but not as vertical as that suggested for Dugong.

The introduction of a lateral component into the masticatory cycle necessitates a slightly different muscle arrangement to that present in Dugong. A lateral movement of the mandible can be produced by a contraction either of the masseter and pterygoid muscles of one side or of the temporal

muscle of the opposite side (Savage, 1959). The almost vertical position of the internal pterygoid muscles of Trichechus makes them inefficient as generators of lateral motion, but the masseter and temporal muscles can produce this lateral movement because of their lengthened effort lever arms.

The mandible of Trichechus is not enlarged anteriorly as is that of Dugong, and the digastric musculature may therefore have a more prominent role as a jaw-opening mechanism. The widely separated paroccipital processes of Trichechus may be related to this function.

When the cheek teeth of Trichechus are in occlusion it is evident that the small pads at the front of the jaws will also be in contact. Transverse motion between these two pads would help to comminute the food plants, but the greater part of this process would be carried out by the cheek teeth. Food is guided towards, and into, the mouth by the forelimbs and by the prehensile lips (Nishiwaki, 1972).

Eocene sirenians

The teeth of the Eocene sirenians that I have examined are worn in a similar way to those of Trichechus. Together with the basic resemblance in skull and mandible morphology between these two groups, this indicates that the method of mastication was much the same also. The masseter and internal pterygoid muscles are prominently indicated on the skulls of all the Eocene genera, and were suitably placed to produce the required lateral movement of the mandible. The digastric muscle was probably more important as a jaw-opening muscle than it is in the recent sirenians (especially Dugong) because it had a more anterior insertion.

Looking at the order as a whole it can be seen that the sirenian feeding mechanism has undergone some important functional changes during the evolution of the group. Leaving aside the extreme dental specializations that can be observed in later members of the order, it is possible to recognise

two major pathways leading to the two superfamilies of modern sirenians.

The members of the Dugongoidea have diverged the most from the structure of the primitive Eocene sirenians. Although they have retained the structure of the posterior parts of the Eocene sirenian skull and mandible in an almost unchanged condition, the dugongoids are noted for the highly modified nature of the anterior region of the jaws. This situation, already incipient in the Eocene genera, is accompanied by the progressive reduction of the dentition. This evolutionary pathway can be followed to the present-day Dugong and its recently extinct relative Steller's Sea Cow, Hydrodamalis gigas.

The second pathway is very meagrely represented in the fossil record. Unlike in the previous superfamily, the modifications occur on the posterior part of the mandible - the horizontal rami and mandibular symphysis being very similar to those of the Eocene forms. This pathway leads to the modern manatees, Trichechus spp., showing that the two modern superfamilies, the Dugongoidea and the Trichechoidea, have been separate since the Eocene.

SELECTED BIBLIOGRAPHY

BOAS, J.E.V. & PAULLI, S. 1908. The elephant's head. First Part. 80pp. Copenhagen.

BOAS, J.E.V. & PAULLI, S. 1925. The elephant's head. Second Part. 51pp. Copenhagen.

EALES, N.B. 1926. Anatomy of the head of a foetal African elephant, Elephas africanus (Loxodonta africanus). Trans. R. Soc. Edinb. 54: 491-551.

FENART, R. 1963. Note sur l'étude du crâne de Halicore dugong par la méthode vestibulaire. Mammalia. 27: 92-98.

FREUND, L. 1908. Beiträge zur Entwickelungsgeschichte des Schädels von Halicore dugong Errl.. Denkschr. med.-naturw. Ges. Jena, 7: 557-625.

GOHAR, H.A.F. 1957. The Red Sea dugong. Publs mar. biol. Stn Ghardaqa, 9: 3-49.

GRASSÉ, P.-P. 1968. Traité de Zoologie. 16 (2). 870pp. Paris.

HILL, W.C.O. 1945. Notes on the dissection of two dugongs. J. Mammal., 26: 153-175.

MAYNARD SMITH, J. & SAVAGE, R.J.G. 1959. The mechanics of mammalian jaws. Sch. Sci. Rev., 141: 289-301.

NISHIWAKI, M. 1972. General Biology. In Ridgway, S.H. (Ed.). Mammals of the sea: biology and medicine: 3-204. Springfield.

SIMPSON, G.G. 1932. Fossil Sirenia of Florida and the evolution of the Sirenia. Bull. Am. Mus. nat. Hist., 59: 419-503.

TURNBULL, W.D. 1970. Mammalian masticatory apparatus. Fieldiana. Geol., 18: 149-356.

WOODARD, J.C. 1969. Personal communication. In Caldwell, D.K. & Caldwell, M.C. 1972. Senses and communication. In Ridgway, S.H. (Ed.). Mammals of the sea: biology and medicine: 466-502. Springfield.

APPENDIX

MUSCLE DATA

	M(g)	M(%)	L	X	H	a	l'	l''
M.m.	266.2	60.0	53°	76°	45°	16.4	12.8	22.4
M.t.	96.4	22.0	48°	45°	70°	6.7	"	"
M.p.e.	18.1	4.1	37°	10°	35°	3.1	"	"
M.p.i.	60.5	13.9	9°	75°	10°	15.7	"	"

M(g) = weight of muscle in grams
M(%) = weight expressed as percentage
L = angle that muscle axis makes with long. plane
X = " " " " " " trans. "
H = " " " " " " horiz. "
a = effort lever arm
l' = resistance lever arm for cheek teeth
l'' = " " " " jaw pads

Useful Power, $E = M(\%) \times F_L \times F_X \times r$

F_L = sine function of L
F_X = " " " X
} correction factors

$r = \frac{a}{l}$

SUGGESTED SIRENIAN PHYLOGENY